

Lopingian (Late Permian) trilobites from the North Caucasus, Russia, with an overview of their distribution worldwide

Eduard V. Mychko

ABSTRACT

Trilobites from the Upper Permian (Changhsingian) of the North Caucasus, previously described by Weber (1944), are revised. *Brachymetopus* (?) *caucasicus* Licharew in Weber, 1944, known only from its pygidium, belongs to the *Brachymetopus* (*Acutimetopus*), and not *Cheiropyge*, as some researchers believed, since it lacks a terminal lobe, characteristic of *Cheiropyge*. A new species *Paraphillipsia urushtensis* sp. nov. has been described. For the first time, photographs of all specimens of the type series of the new species are presented. *Kathwaia capitorosa* Grant, 1966, described from the Wuchiapingian of Pakistan, does not have significant morphological differences from the North Caucasian *K. caucasica* (Weber, 1944) and is here considered a junior subjective synonym of the latter. Other trilobite assemblages of the North Caucasus are represented by *Pseudophillipsia solida* Weber, 1944, *Ps.* (?) *caucasica* Weber, 1944 and *Ps.* (?) cf. *mustafensis* Tumanskaya, 1935. It is proposed not to use the subgenus *Pseudophillipsia* (*Nodiphillipsia*) based on its redundancy. The “problem of similar pygidia” of *Pseudophillipsia* and *Ditomopyge* (*Carniphillipsia*) is discussed. It is proposed to conditionally classify all species known exclusively from highly segmented pygidia as *Pseudophillipsia*. All currently known localities of Lopingian trilobites in the World are considered, and their stratigraphical occurrences are clarified. This list is supplemented by localities from Crimea, Far East, Hungary, New Zealand and Spitsbergen. The latter localities indicate that Lopingian trilobites were not limited to the Palaeo-Tethys, but were present in mid-latitudes. Trilobites of the Lopingian were not as diverse as in the Guadalupian and were represented by only nine (probably 10) genera and 36 species (and species determined in open nomenclature). This time interval is characterized by an extremely low rate of origination of new genera and a high rate of extinction.

Eduard V. Mychko. Shirshov Institute of Oceanology, Russian Academy of Sciences, Nahimovskiy prospekt 36, Moscow, 117997, Russia. Scientific and Educational Center “Environmental geology and Maritime Management”, Immanuel Kant Baltic Federal University, Nevskogo Street 14, Kaliningrad, 236016, Russia.

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INTRODUCTION

Widely distributed and numerous in Early Palaeozoic, trilobites decreased in diversity from benthic communities in post-Devonian times. Trilobites survived in Carboniferous and Permian, becoming extinct during the Great Permian Extinction. Therefore, in deposits of the Permian, remains of these arthropods are relatively rare and their diversity is low. Unfortunately, due to the rarity and impossibility of using this group to solve biostratigraphical problems, Late Palaeozoic trilobites turned out to be one of the least studied groups.

Analyzing studies of Lopingian trilobites of the World, it becomes obvious that the overwhelming number of articles are episodic and regional, and comprehensive works covering all known species of this era are practically absent. In fact, research work on Lopingian trilobites can be divided into countries: Slovenia (Hahn et al., 1970), Hungary (Schréter, 1948), Iran (Hahn and Hahn, 1981; Lerosey-Aubril, 2012), Pakistan (Grant, 1966), China (Diener, 1897; Lu, 1974; Qian, 1977; Yin, 1978; Qian, 1981; Zhang, 1982, etc.), Indonesia (Beyrich, 1865; Hahn and Brauckmann, 1975; Brauckmann and Gröning, 2013), Japan (Kobayashi and Hamada, 1984a; 1984b), Thailand (Kobayashi and Sakagami, 1989), and Spitsbergen (Kobayashi, 1987; Bruton, 1999). There are very few generalized studies that provide lists and distribution of known trilobites of the Lopingian. Here I should mention the works of Owens (1983; 2003), as well as the summary article by Hahn, Hahn and Brauckmann (2001).

Major studies of Permian (and Carboniferous) trilobites in Russia were carried out over 80 years ago (Toumanský, 1930; Tumanskaya, 1935; Weber, 1932; 1933; 1937; 1944). Since then, trilobites of this age have been hardly studied by Soviet and Russian palaeontologists, except for several works by the author (Mychko, 2012; Mychko and Alekseev, 2017; Mychko and Savchuk, 2019; Mychko, 2023, etc.), as a result of which the systematic position and stratigraphic the distribution of previously described taxa requires revision in accordance with modern ideas. In addition, over

the past decades, a fairly large amount of new, not yet described factual material has accumulated.

The most important and major revision of the Carboniferous–Permian trilobites of the World (including the territory of former USSR) was carried out by German palaeontologists over almost half a century (Hahn and Hahn, 1969; 1970; 1972; 1993; 1996; 2008; 2015; 2016; Hahn et al., 2019). These publications revised almost all known Carboniferous and Permian trilobites. Of course, it was quite difficult to cover such a large amount of data, and the authors of these revisions could not personally familiarize themselves with the material stored in the USSR (Russia), but, nevertheless, the cited works can be considered key for the study of modern ideas about the taxonomy and synonymy of many species of trilobites Carboniferous and Permian.

The trilobites of the North Caucasus studied in this article were first described by the Soviet palaeontologist Weber in his fundamental work on the Permian trilobites of the USSR (1944), published posthumously. Over a long period of time, the Caucasian species and species determined in open nomenclature described in this study were partially revised by Hahn and Hahn. However, neither Weber's original publication nor the Hahn's catalogues provided photographs of all specimens of the type series of these trilobites, and many taxonomic questions require clarification in the light of new data. An equally important aspect of this publication is not only a systematic revision, but also a clarification of the age of the host deposits. The age of the discussed North Caucasian trilobites has varied among different authors from the Cisuralian, to the Guadalupian and Lopingian (Figure 1). The latest data (*see the Localities section*) confidently support the Lopingian age.

LOCALITIES

Permian trilobites of the North Caucasus are confined to the upper Changhsingian formations, exposed a number of localities in the basins of the Belaya River, Bol'shaya Laba River and Malaya Laba River in its north-western part (Figure 2). The

Ma	ISC			Russian and Ural regional units		Tethyan regional stages		South China regional units		Western European series	North America series					
	System	Series	Stages	Series	Stages	Pamirs	Salt Range	Series	Stages							
	252	Permian	Lopingian	Changhsingian	Tatarian	Vyatkian	Dorashamian	Chhidru	Changshingian	Meishanian Baoqingian	Bundsandstein	Ochoan				
254	Wuchiapingian			Severodvinian			Midian	Kalabagh	Wargal	Wujiapingian	Laoshanian		Zechstein			
255	Capitanian							Birmian		Urzhumian	Murgabian			Maokouian	Laibinian	
256	Wordian		Kazanian	Kubergandian	Sardhai	Chinsian	Lengwuan		Rotliegend							
257	Roadian						Ufimian	Kungurian		Bolorian	Warchha		uncertain limit	uncertain limit		
258	Cisuralian		Cisuralian	Kungurian	Yakhtashian	Warchha			Chuanhsanian				Xiangboan	Leonardian		
259							Artinskian	Artinskian		Yakhtashian	Warchha		Chuanhsanian		Luodianian	
260															Sakmarian	Sakmarian
261							Asselian	Asselian		Asselian	Tobra		Chuanhsanian			
262															Asselian	Asselian

FIGURE 1. Stratigraphic subdivision of the Permian system according to the International Stratigraphic Scale (ISC) 2023 and correlation with regional divisions. Built in the program TSCreator version 8.1, with various additions and changes by the author.

famous Russian geologist Robinson discovered these outcrops in 1912, and later (Robinson, 1932) based on the Chernyshev's determinations of brachiopods, considered them to be Cisuralian. With the advent of monographic descriptions of brachiopods and bivalves, Likharev determined the age of these deposits as Lopingian, more precisely post-Kungurian on the modern stratigraphic scale (Kotlyar et al., 2004).

The stratigraphy of the Permian deposits of the Northwestern Caucasus was described by Miklouho-Maclay (1954, 1956), who, based on lithology and foraminiferal assemblages, established four formations (later Triassic ammonoids were discovered in one of these formations). The three Permian formations are: Kutanskaya (basal conglomerates and sandstones with some limestone interbeds in the upper part), Nikitino (laminated algal limestones with abundant foraminifera) and

Urushten (reef limestones and shales) (Kotlyar et al., 2004).

Studies of fossils from these deposits have yielded varying age estimates. Brachiopod assemblages were dated from the Midian–Dorashamian (Figure 1) of Tethyan scale (Grunt and Dmitriev, 1973; Kotlyar et al., 1983; Kotlyar, 1989); ammonoids of the Urushten Formation were dated to the cis-Dzhulfian interval of the Tethyan scale (Bogoslovskaya, 1984), and foraminifera to the cis-Dorashamian of the Tethyan scale (Kotlyar et al., 1983). Later Kotlyar et al. (1999a), as well as Pronina-Nestell and Nestell (2001) established that the age of these deposits is Late Changhsingian (International Stratigraphical Chart). According to Pronina-Nestell and Nestell (2001) in the Lopingian of the North Caucasus, there are small foraminifera and fusulinaceans, characteristic of the zones *Palaeofusulina sinensis* = *Palaeofusulina nana* and *Colaniella parva* of the Late Changhsingian of



FIGURE 2. Main Lopingian sections of the North Caucasus: **A** – Urushten; **B** – Gefo Mountain; **C** – Khamyshki (Raskol-Skala Mountain); **D** – Nikitinskaya Ravine; **E** – Khuko Mountain; **F** – Beskos; **G** – Severnaya Ravine; **H** – Armovka Ravine.

Palaeo-Tethys, and therefore these deposits can be attributed to this age.

The Upper Changhsingian formations of the Northwestern Caucasus are placed in the Belalabino Group (Figure 3), which is separated from the underlying and overlying deposits by erosional unconformities. These formations contain diverse and abundant algae, foraminifera, sponges, brachiopods, bivalves and gastropods, ammonoids and trilobites (Kotlyar et al., 2004).

In total, only five localities of Lopingian trilobites are known in the North Caucasus (Figure 2). These were previously characterized in the works of Mychko and Alekseev (2017). The information below has been clarified and supplemented.

Urushten (Figures 2A, 3). Krasnodar Krai, Mostovsky district, Malaya Laba River basin, Urushten tract (=paraje) and Urushten River. In the Malaya Laba River basin, south from the Urushten, in the

deposits of the Upper Formation (P_1^b) Robinson (1932, p. 23) discovered trilobites, which Weber originally identified as *Proetus postcarbonarius* Gemm., *Pr. ? semipustulatus* Weber in Robinson, 1932 and *Phillipsia tschernyschewi* (Netschaew in Weber, 1932).

These findings, as well as material collected from here by Likharev, were later described by Weber as *Paraphillipsia karpinskyi* Tumanskaya, 1935 (Weber, 1944, p. 12, table 1, figs. 18–20, 22), *Pseudophillipsia elegans* var.? (Weber, 1944, p. 13, table 2, fig. 2), *P. (?) solida* Weber, 1944 (Weber, 1944, p. 13, table 2, figs. 8, 9) and *Proetus girtyi* var. *caucasica* Weber, 1944 (Weber, 1944, p. 15, fig. 17).

A different list for the Urushten Formation of the North Caucasus according to earlier definitions by Weber was given by Miklouho-Maclay (1956, p. 71): *Proetus postcarbonarius* Gemmellaro, 1892,

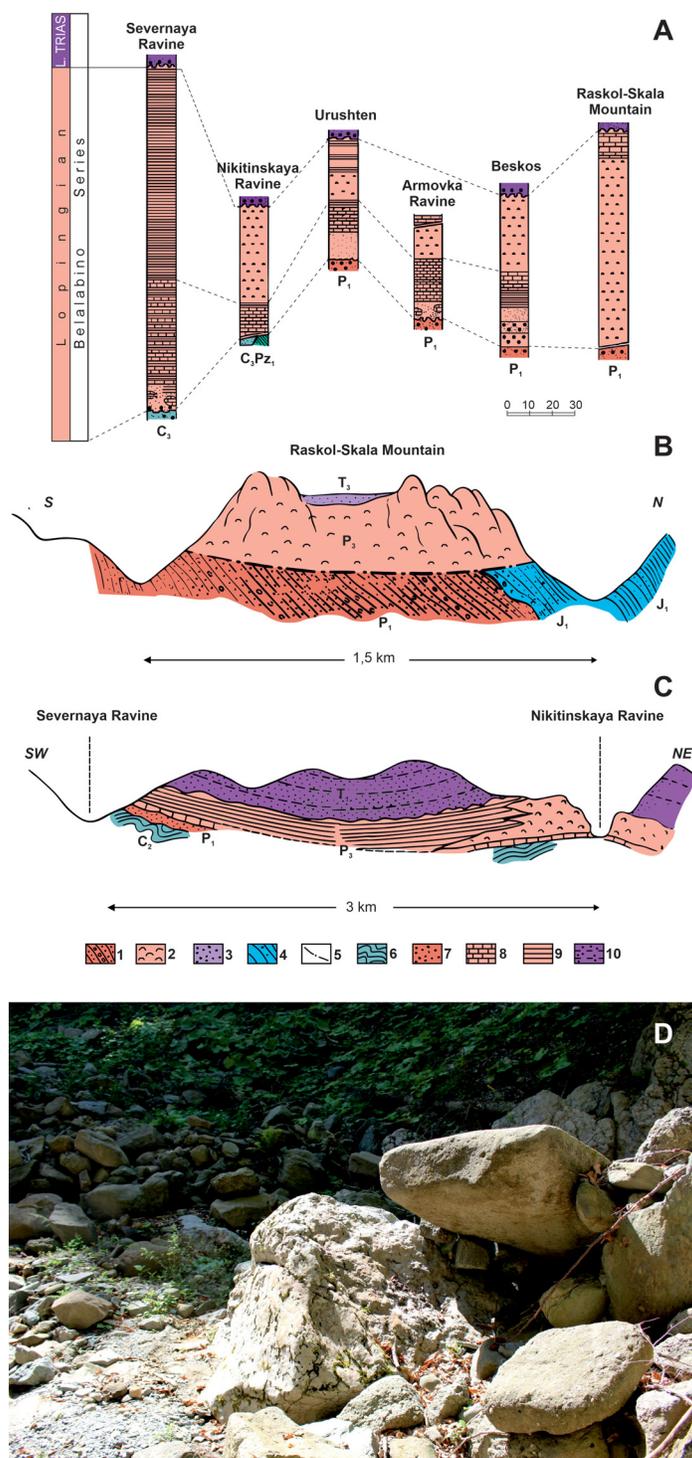


FIGURE 3. Lopingian sections of North Caucasus: **A** – The main Lopingian sections of the Malaya Laba and Bolshaya Laba basins in the North Caucasus, according to Kotlyar et al. (2004). **B** – the schematic profile across Raskol-Skala Mount near the village of Khamyshki according to Miklouho-Maclay (1956) with modifications. **C** – the schematic profile across the Severnaya and Nikitinskaya ravines, on the right bank of the Malaya Laba River; according to Miklouho-Maclay (1956) with modifications. **D** – reef limestones of the Urushten Formation in Nikitinskaya ravine, photo by author, 2019. **1** – Cisuralian red conlomerates and sandstones; **2** – reef limestones of the Urushten Formation; **3** – Upper Triassic sandstones; **4** – Lower Jurassic sandstones and shales; **5** – thrust line; **6** – Pennsylvanian sandstones and shales; **7** – Cisuralian sandstones and conlomerates; **8** – algal-foraminiferal limestones of the Nikitino Formation; **9** – clay shales of the Urushten Formation; **10** – Lower Trias sandstones.

Pr. semipustulatus Weber in Robinson, 1932, *Phillipsia tschernyschewi* (Netschaew in Weber, 1932), *Pseudophillipsia elegans* Gemmellaro, 1892. Apparently, the monograph by Weber (1944), devoted to the description of the Permian trilobites of the USSR, was unfamiliar to her. In the older *Nikitino Formation*, Miklouho-Maclay did not mention trilobites.

Likharev (1939, p. 200) for the Permian of the North Caucasus (the Malaya Laba River basin) cited only *Proetus? girtyi* Tumanskaya, 1935.

Brachiopods *Scacchinella jakovlevi*, *Leptodus richthofeni* and *Camarophoria caucasica*, found together with trilobites, belong to the assemblage of the Urushten Formation (Kotlyar et al., 1983).

Mountain Gefo (Figure 2B). Republic of Adygea, Maikop district, Belaya River basin. The work of Robinson (1932, p. 24) provides a list of Likharev's fauna in the light limestones of the Upper Formation (P₁^b) near Mountain Gefo.

It includes a mention of the discovery of the trilobite *Pseudophillipsia elegans* Gemmellaro, 1892 (definition by Weber) and foraminifera *Palaeofusulina nana*, characteristic only of the Urushten Formation (Miklouho-Maclay, 1954; Kotlyar et al., 1983).

Likharev found near Mount Gefo, in blocks of limestone along the Tegen' River (outcrop No. 30) the following: *Griffithides (Neogriffithides) cf. almensis* Tumanskaya, 1935 (Weber, 1944, p. 11, table 1, fig. 15), *Pseudophillipsia elegans* var. *caucasica* Weber, 1944 (Weber, 1944, p. 12, table 2, fig. 4), *Ps. mustafaensis* Tumanskaya, 1935? (Weber, 1944, p. 13, table 2, fig. 3) and *Ps. (?) solida* Weber, 1944 in outcrop No. 33 (Weber, 1944, p. 14).

Khamyshki (Figures 2C, 3). Republic of Adygea, Maikop district, Belaya River basin. Around this village, near Raskol Rock (mountain), in the western part of the block (outcrop No. 42c) Likharev discovered *Griffithides (Neogriffithides) cf. almensis* Tumanskaya, 1935 (Weber, 1944, p. 11, table 1, fig. 16) and *Proetus girtyi* var. *caucasica* Weber, 1944 (Weber, 1944, p. 15, table 2, fig. 16). In this locality, limestones of the Urushten Formation are exposed (Kotlyar et al., 1983; Kotlyar et al., 2004).

Nikitinskaya ravine (Figures 2D, 3). Krasnodar Krai, Mostovsky district. Malaya Laba River basin. Likharev found the pygidium of *Paraphillipsia karpinskyi* Tumanskaya, 1935 at this locality, 2.25 km above its entrance (Weber, 1944, p. 12), in the same place in the scree of *Pseudophillipsia elegans* var.? (Weber, 1944, p. 13), and not far from

this locality in a block (outcrop No. 842) Robinson discovered the pygidium of *Brachymetopus (?) caucasicus* Licharew in Weber, 1944 (Weber, 1944, p. table 2, fig. 15). In this locality, deposits of the *Nikitino* and *Urushten* formations are exposed (Kotlyar et al., 1983; Kotlyar et al., 2004).

Attempts to isolate conodonts from the samples collected here by Grunt and transferred to the Department of Palaeontology of Lomonosov Moscow State University (Russia), after many years of dissolution were successful – single elements of the shallow-water genus *Hindeodus* were found (personal commun. by Prof. A.S. Alekseev, 02.20.2024). In the same samples, an unidentified pygidium, about 1 mm in length, with about six rings in the axis, but lacking ribs on the pleural lobes as recovered; it appears to be a larval stage, perhaps a meraspis. The search for trilobites in this locality by author and M.S. Boiko in 2019 was unsuccessful: when visiting the locality (Figure 3D), it turned out that a mountain road had been built through it. The remaining outcrops contained rare fossils, in particular a few brachiopods.

Mountain Khuko (Figure 2E). Krasnodar Krai, Sochi urban district, southern slope of the Greater Caucasus. On the northeastern slope of Khuko Mountain in the axial part of the Greater Caucasus Range, in the “calcareous-terrigenous sequence” or Khuko Formation (Vyalov, 1934), and according to Miklouho-Maclay (1952, p. 12) – in the *Nikitino* Formation, the trilobite *Pseudophillipsia* sp. was found together with brachiopods (Belov, 1967, p. 89). Belov considered the age of this strata to be Cisuralian (Artinskian). These deposits near the Mountain Khuko were also noted by Miklouho-Maclay (1956, p. 61).

SYSTEMATIC PALAEONTOLOGY

About the systematics. In the Permian, trilobites of three proetid families are found: Phillipsiidae, Proetidae and Brachymetopidae. The first, Phillipsiidae, are the most numerous and diverse, the second and third are rare. To a first approximation, the morphology of these three families seems very different (for example, fused facial sutures in many Brachymetopidae), which may lead to agree with Adrain (2011) about the relationship of these families in two different orders. However, the author adheres to the opinion of Lamsdell and Selden (2014) and considers it necessary to leave the division of the order Proetida into two superfamilies Aulacopleuroidea and Proetoidea.

The Permian Phillipsiidae includes the following subfamilies: Ditomopyginae, Bollandiinae and

Cummingellinae; for the Permian Proetidae, subfamilies have not been established, and Brachymetopidae in the Permian are represented by only one subfamily, Brachymetopinae.

About subspecies. In further revision, the author is of the opinion that the use of subspecies in taxonomic studies of fossil organisms is redundant (Burbrink et al., 2022). Subspecies (and varieties) previously established by other authors are considered here as independent species.

About the storage location. All studied specimens of trilobites from the Lopingian of the North Caucasus are stored in the collections of the Chernyshev Central Geological Research Museum (CNIGRMuseum) in St. Petersburg (Russia). The holotype of *Kathwaia capitorosa* is kept in the palaeontological collection of the Smithsonian National Museum of Natural History (USNM) in Washington (USA). One specimen of *Pseudophillipsia solida* is kept in the collection of the Geological and Palaeontological Institute of the University of Ljubljana (GPIUL) in Slovenia.

Abbreviations. Cc – complete exoskeleton, Cph – cephalon, Cr – cranidium, Gl – glabella, Lg – librigena (=free cheek), Py – pygidium, Hy – hypostome.

- Order PROETIDA Fortey and Owens, 1975
 Superfamily AULACOPLEUROIDEA Angelin, 1854
 Family BRACHYMETOPIDAE Prantl and Přibyl, 1950
 Subfamily BRACHYMETOPINAE Prantl and Přibyl, 1950
 Genus BRACHYMETOPUS McCoy, 1847
 Subgenus BRACHYMETOPUS (ACUTIMETOPUS) Hahn and Hahn, 1985
- 1985 *Brachymetopus (Acutimetopus)* – Hahn and Hahn, p. 445, 460, 461, 465, 474, 476, 477, Abb. 9.
 1987 *Brachymetopus (Acutimetopus)* – Gandl, p. 6, 10, 48, 49, 53–54.
 1987 *Brachymetopus (Acutimetopus)* – Hahn and Hahn, p. 573, 574.
 1989a *Brachymetopus (Acutimetopus)* – Hahn, Hahn, and Schneider, p. 650.
 1989b *Brachymetopus (Acutimetopus)* – Hahn, Hahn, and Yuan, p. 113, 119, 121, 123, 124, 126.
 1993 *Brachymetopus (Acutimetopus)* – Owens and Hahn, p. 170, 173.
 1994 *Brachymetopus (Acutimetopus)* – Brauckmann, p. 30.

- 1996 *Brachymetopus (Acutimetopus)* – Hahn and Hahn, p. 8, 35, 38, 39, 40–42, 44, 47, 50, 52, 56, 62, 65, 146, 153, 154.
 1996 *Brachymetopus (Acutimetopus)* – Hammel, p. 751.
 2003 *Acutimetopus* – Jell and Adrain, p. 337.
 2011 *Brachymetopus (Acutimetopus)* – Gandl, p. 103–106.
 2016 *Brachymetopus (Acutimetopus)* – Mychko, p. 34, 61, 136, 141, 152–153.
 2019 *Brachymetopus (Acutimetopus)* – Mychko and Savchuk, p. 346, 347, 348, 349.
 2021 *Brachymetopus (Acutimetopus)* – Flick and Shiino, p. 91, 92, 97, 99.
 2023 *Brachymetopus (Acutimetopus)* – Brezinski, p. 3, 9–11, 15, 16.

Type species. *Cheiropyge kansasensis* Weller, 1944; Upper Pennsylvanian, upper part of the Haskell Limestone (or Cass Formation, the upper part of the Kasimovian, see: Heckel, 1999; Heckel et al., 2007); USA, Kansas, Leavenworth; designated by Hahn and Hahn (1985, p. 445).

Diagnosis. Cephalon elongated, subtriangular, with an apical peak and genal angles (often rounded, but some species have short genal spines); covered with tubercles; facial sutures ankylosed; glabella cylindrical, moderate to long, tapering towards the anterior part, bears poorly developed small L₁-lobes; preglabellar field wide; eyes medium-sized, set towards back of cephalon; pygidium elongated, often with marginal spines on the extensions of pleural ribs; pygidial axis long, has 18 or more axial rings, and 6–7 pleural ribs; sometimes there is a post-axial spine.

Comparison. From other subgenera *Brachymetopus (Acutimetopus)* differs mainly in the subtriangular outline of the cephalon due to the presence of an apical peak in the anterior part, which makes it similar to *Cheiropyge*. It differs from the latter in the absence of a swollen terminal lobe in the posterior part of the pygidium.

Remarks. It is necessary to provide a list of the remaining subgenera of *Brachymetopus* because two of them, after their description, turned out to be homonyms, but some authors continue to use the same names. Thus, *Brachymetopus* includes the nominate subgenus *B. (Brachymetopus)* McCoy, 1847 (Upper Devonian – Upper Pennsylvanian of Eurasia, North America and Australia), *B. (Acutimetopus)* Hahn and Hahn, 1985, *B. (Spinimetopus)* Hahn and Hahn, 1985 (Mississippian of Eurasia and Australia), *B. (Conimetopus)* Hahn and Hahn, 1985 (Mississippian – Cisuralian of Eur-

asia and North America) and *B. (Hahnus) Özdikmen*, 2009 (Mississippian of Eurasia), which should be considered a synonym of *B. (Eometopus)* Hahn and Hahn, 1996 and *B. (Narinia)* Archbold, 1997 (Guadalupian of Asia), which is a synonym of *B. (Iriania)* Archbold, 1981.

Species. 16 species and two species determined in open nomenclature (Table 1).

Occurrence. Pennsylvanian (Bashkirian) – Lopingian (Changhsingian); Eurasia, Arctic and North America.

Brachymetopus (Acutimetopus) caucasicus
Licharew in Weber, 1944
Figure 4

- 1944 *Brachymetopus (?) caucasicus* – Weber, p. 15,18, pl. II, fig. 15a–b.
1969 *Cheiropyge? caucasica* – Hahn and Hahn, p. 41–42.

TABLE 1. Known species of *Brachymetopus (Acutimetopus)* Hahn and Hahn, 1985. Permian species are highlighted in bold. Here and below is a list of species according to their year of description.

Species	Part	Stratigraphy	Geography
<i>B. (A.) gracilis</i> Heritsch, 1931	Cph	Upper Pennsylvanian, Stephanian (~Kasimovian–Gzhelian)	Austria, Carinthia
<i>B. (A.) moelleri</i> Weber, 1932	Cph	Cisuralian, Asselian	Russia, Perm Krai
<i>B. (A.)</i> sp. Weber, 1937	Cph	Middle Pennsylvanian, Moscovian	Donetsk Basin, Krasnaya Mogila railway station
<i>B. (A.) caucasicus</i> Licharew in Weber, 1944	Py	Lopingian, Changhsingian	Russia, Krasnodar Krai, Malaya Laba River Basin
<i>B. (A.) kansasensis</i> (Weller, 1944) type species	Cc	Upper Pennsylvanian (U. Pennsylvanian), upper part of the Haskell Limestone	USA, Kansas, Leavenworth County
<i>B. (A.) pseudometopina</i> Gauri et Ramovš, 1964	Cph, Py	Upper Pennsylvanian, Gzhelian	Slovenia, Southern Karavanke
<i>B. (A.) weberi</i> Osmólska, 1968	Cph	Upper Pennsylvanian, Kasimovian	Russia, Vaigach Island
<i>B. (A.) jesenicianus</i> Hahn et Hahn in Hahn, Hahn et Ramovš, 1977	Cc, Cph, Py	Upper Pennsylvanian, Gzhelian	Slovenia, Southern Karavanke
<i>B. (A.)</i> sp. Zhang, 1983	Py	Pennsylvanian (?)	China, Xinjiang Uyghur Autonomous Region
<i>B. (A.) chamberlaini</i> (Kobayashi et Hamada, 1984a)	Py	Cisuralian, L. Wolfcampian (~Asselian), Phelan Creek Formation	USA, Alaska, vicinity of the Gulkan glacier
<i>B. (A.) macgrathensis</i> Hahn et Hahn, 1985	Cph, Py	Upper Pennsylvanian – Cisuralian (Asselian)	USA, Alaska, Cheeneetnuk River Basin
<i>B. (A.) edwardsi</i> Owens, 1986	Cph, Py	Lower Pennsylvanian, Kinderscoutian (~lower part of the Bashkirian)	England, West Yorkshire
<i>B. (A.) spinicauda</i> Gandl, 1987	Cph, Py	Pennsylvanian, Namurian B – Westphalian (~Bashkirian–Moscovian)	Spain, Cantabrian Mountains, Palencia
<i>B. (A.) acuticeps</i> Gandl, 1987	Cph, Py	Lower Pennsylvanian, Namurian C (~upper part of the Bashkirian)	Spain, Cantabrian Mountains, Leon
<i>B. (A.) asiaticus</i> Hahn, Hahn et Yuan, 1989	Cph, Py	Lower Pennsylvanian, Dala Formation (~upper part of the Bashkirian)	China, Guangxi Zhuang Autonomous Region, Nandan County
<i>B. (A.) junggarensis</i> Wu et Feng, 1991	Py	Upper Pennsylvanian, Shiqiantan Formation	China, Xinjiang Uygur Autonomous Region, Dzungaria
<i>B. (A.) kalodermatus</i> Hahn et Hahn, 1992	Cph, Py	Lower Pennsylvanian, M. Morrowan – M. Atokan (~Bashkirian)	USA, Alaska, Alexander Archipelago
<i>B. (A.) phalanx</i> Gandl, 2011	Cph, Py	Middle Pennsylvanian, Westphalian D (~upper part of the Moscovian)	Spain, Cantabrian Mountains, Palencia

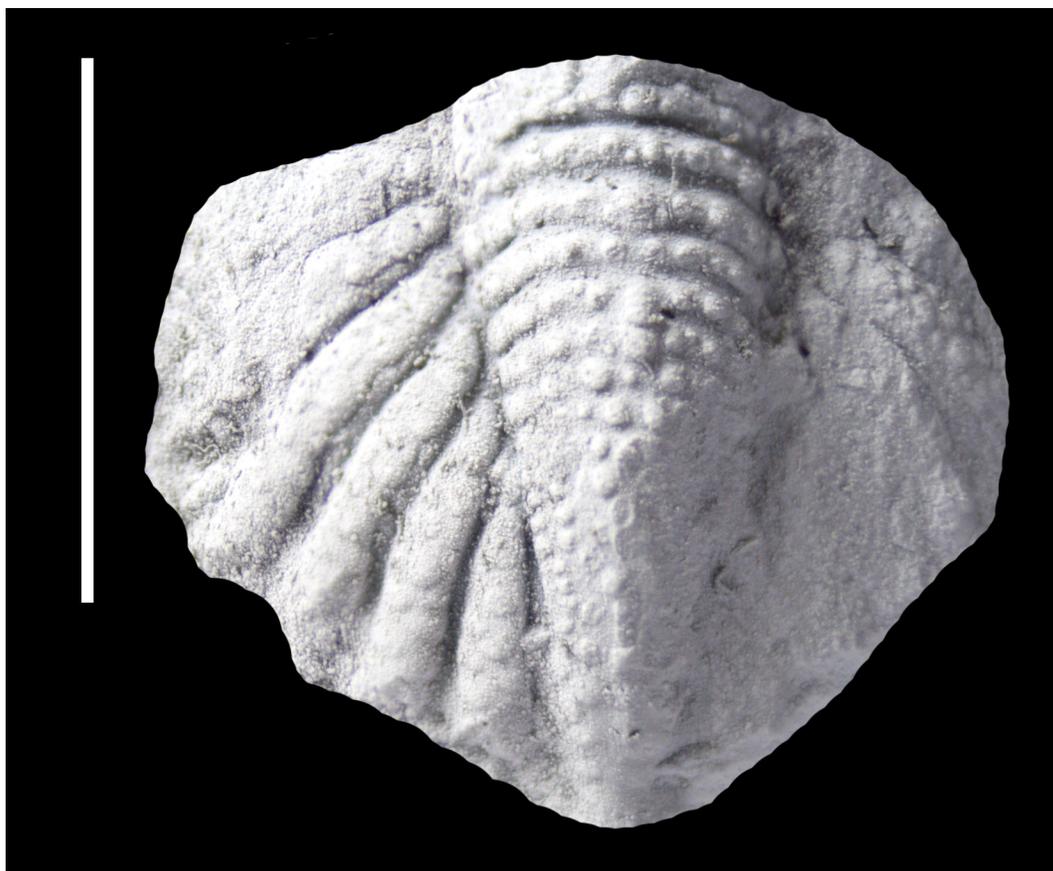


FIGURE 4. Pygidium of *Brachymetopus (Acutimetopus) caucasicus* Licharew in Weber, 1944; CNIGRMuseum, No. 86/5217; Lopingian, Changhsingian, *Urushten* or *Nikitino* formation; Russia, Krasnodar Krai, Malaya Laba River, Nikitinskaya Ravine. Scale bar equals 5 mm.

- | | | | |
|-------|--|-------|---|
| 1975 | <i>Cheiropyge? caucasica</i> – Hahn and Hahn, p. 17. | 1989b | <i>Brachymetopus (Acutimetopus) caucasicus</i> – Hahn, Hahn, and Yuan, p. 125. |
| 1978 | <i>Cheiropyge? caucasica</i> – Koizumi and Sasaki, p. 299. | 1992 | <i>Brachymetopus (Acutimetopus) caucasicus</i> – Hahn and Hahn, p. 117. |
| 1981 | <i>Brachymetopus (?) caucasicus</i> – Archbold, 1981, p. 36,37. | 1992 | <i>Brachymetopus caucasicus</i> – Brezinski, p. 928. |
| 1981 | <i>Cheiropyge? caucasica</i> – Přibyl and Vaněk, p. 187–188. | 1996 | <i>Brachymetopus (Acutimetopus) caucasicus</i> – Hahn and Hahn, p. 43–44, abb. 51. |
| 1983 | <i>Brachymetopus caucasicus</i> – Owens, p. 34. | 2011 | <i>Brachymetopus (Acutimetopus) caucasicus</i> – Gandl, p. 103. |
| 1984a | <i>Brachymetopus (?) caucasicus</i> – Kobayashi and Hamada, p. 37. | 2016 | <i>Brachymetopus (Acutimetopus) caucasicus</i> – Mychko, p. 153, pl. I, fig. 4a–b. |
| 1984a | <i>Cheiropyge? caucasica</i> – Kobayashi and Hamada, p. 25,29,33,38,39. | 2017 | <i>Brachymetopus (?) caucasicus</i> – Mychko and Alekseev, p. 68. |
| 1985 | <i>Brachymetopus (Acutimetopus?) caucasicus</i> – Hahn and Hahn, p. 465,468. | 2019 | <i>Brachymetopus (Acutimetopus) caucasicus</i> – Mychko and Savchuk, p. 348, fig. 1d,e. |
| 1986 | <i>Brachymetopus caucasicus</i> – Owens, p. 13. | 2021 | <i>Cheiropyge? caucasica</i> – Flick and Shiino, p. 92. |
| 1987 | <i>Brachymetopus (Acutimetopus) caucasicus</i> – Gandl, p. 53. | | |

Holotype. CNIGRMuseum, No. 86/5217, incomplete pygidium; *Urushten* or *Nikitino* Formations,

Changhsingian, Lopingian; Nikitinskaya Ravine, Malaya Laba River, Krasnodar Krai, Russia; discovered by Robinson in 1924; Weber, 1944, pl. II, fig. 15; designated by monotype.

Description. Pygidium slightly convex, subtriangular, elongated (L/W = 0.6); pygidial axis in anterior part equal in width to lateral lobes, strongly narrowing towards the posterior end of pygidium; number of axial rings is about 20 (15 anterior rings clearly visible, then rings merge, but their number >5); rings with flattened tubercles; first, third and fifth rings each have one large central tubercle; on anterior rings the number of tubercles – 8; furrows between rings deep; lateral lobes uniformly convex, with 6 pair pleural ribs, semicircular in cross-section, without pleural furrows; ribs located at an angle gradually decreasing towards posterior end of pygidium, so that last rib almost parallel with axis; interpleural furrows very deep and wide; widen towards the edge of pygidium; ribs bear numerous small tubercles; apparently, ribs ended with spines (which are not visible on the holotype due to incomplete preservation).

Dimensions (in mm). Length of pygidium ~7; width of pygidium ~13(?); width of axis in the anterior part – 3.3; ratio of length to width of pygidium ~0.5; ratio of the width of the axis in the anterior part to the width of the pygidium – 3.9.

Comparison. In terms of the number of axial rings of pygidium is similar to the species *B. (A.) kansasensis* and *B. (A.) weberi*, but differs in a different number of pairs of pleural ribs (*B. (A.) kansasensis* has 6, in *B. (A.) weberi* – 8). It also differs from *B. (A.) kansasensis* in the more triangular shape of the pygidium. It differs from *B. (A.) acuticeps* in the triangular shape of the pygidium, a larger number of axial rings (*B. (A.) acuticeps* has 12 axial rings), the absence of obvious pleural furrows, a narrower axis, and a less steep angle between the pleural ribs and the axis. It differs from *B. (A.) edwardsi* and the closely related species *B. (A.) spinicauda* in a larger number of axial rings (in these species there are up to 18 axial rings) and in the absence of obvious pleural furrows. It differs from *B. (A.) gracilis* in a larger number of axial rings (in *B. (A.) gracilis* there are up to 18 axial rings) and in a smaller number of pleural ribs (in *B. (A.) gracilis* there are seven pairs). It differs from *B. (A.) kalodermatus* by a more triangular shape of the pygidium, a larger number of axial rings (*B. (A.) kalodermatus* has about 15 axial rings), and a more pronounced angle between the pleurae and the axis. It differs from *B. (A.) chamberlaini* in the triangular shape of the pygidium, a larger number

of axial rings (*B. (A.) chamberlaini* has about 12), the absence of obvious pleural furrows, a narrower axis and a larger number of pairs of pleural ribs (in *B. (A.) chamberlaini* there are six). Similar to the closely related species *B. (A.) pseudometopina* and *B. (A.) macgrathensis*, but differs in a larger number of axial rings.

Remarks. Unfortunately, the poor preservation of the specimen does not allow us to establish the morphology of the ends of the pleural ribs of the pygidium, which most likely terminated in spines, as in most members of *Brachymetopus* (*Acutimetopus*). However, from the available material it is noticeable that in the posterior part of the pygidium there is no swollen unpaired terminal lobe, characteristic of the genus *Cheiropyge*. This is important, since some researchers, not having the opportunity to familiarize themselves directly with the holotype and, having only a drawing and photograph from the work of Weber (1944), conditionally classified this species as *Cheiropyge* (e.g., Kobayashi and Hamada, 1984a; Flick and Shiino, 2021, etc.).

The author of the name of this species should be considered Likharev, since he is listed as such in synonymies in the original description of the species (Weber, 1944, p. 15) with the addition that this name was indicated in the collection (“nom. in coll.”).

Occurrence. Lopingian, Changhsingian; North Caucasus (Krasnodar Krai).

Material. Holotype (monotype).

Superfamily PROETOIDEA Hawle and Corda,
1847

Family PHILLIPSIIDAE Oehlert, 1886

Subfamily CUMMINGELLINAE Hahn and Hahn,
1967

Genus PARAPHILLIPSIA Toumansky, 1930

- 1930 *Phillipsia* (*Paraphillipsia*) – Toumansky, 1930, p. 474–476, 477.
- 1935 *Paraphillipsia* – Tumanskaya, 1935, p. 19–20.
- 1935 *Paraphillipsia* – Weller, p. 31–32.
- 1937 *Paraphillipsia* – Gheyselinck, 1937, p. 4, 36, 58, 63.
- 1939 *Paraphillipsia* – Likharev, p. 198.
- 1944 *Paraphillipsia* – Weber, p. 4, 6, 7, 11–12, 17–19.
- 1944 *Paraphillipsia* – Weller, p. 320, 326–327.
- 1955 *Paraphillipsia* – Hupé, p. 208.
- 1959 *Paraphillipsia* – Weller, p. O401.
- 1960 *Paraphillipsia* – Maximova, p. 138.
- 1966 *Paraphillipsia* – Grant, p. 70.

- 1967 *Paraphillipsia* – Hahn and Hahn, p. 337,346.
- 1970 *Paraphillipsia* – Hahn and Hahn, p. 294–295.
- 1975 *Paraphillipsia* – Hahn and Hahn, p. 16,17,57–58.
- 1977 *Paraphillipsia* – Chamberlain, p. 758.
- 1979 *Paraphillipsia* – Kobayashi and Hamada, p. 3,12.
- 1980 *Paraphillipsia* – Haas, Hahn, and Hahn, p. 120.
- 1981 *Paraphillipsia* – Kobayashi and Hamada, p. 4.
- 1982 *Paraphillipsia* – Kobayashi and Hamada, p. 46,47.
- 1983 *Paraphillipsia* – Owens, p. 24,25,26,35–38.
- 1984 *Paraphillipsia* – Hahn, Hahn, and Brauckmann, p. 67.
- 1984a *Paraphillipsia* – Kobayashi and Hamada, p. 3,15,20,23,24,25,26,28,30,44,45,84.
- 1985 *Paraphillipsia* – Hahn and Hahn, p. 448.
- 1989b *Paraphillipsia* – Hahn, Hahn, and Yuan, p. 153,159.
- 1990 *Paraphillipsia* – Hahn, Hahn, and Ramovš, p. 146,154,156,158,160,161.
- 1990 *Paraphillipsia* – Hahn, S. 41.
- 1992 *Paraphillipsia* – Hahn and Hahn, p. 105.
- 1992 *Paraphillipsia* – Brezinski, p. 926.
- 1993 *Paraphillipsia* – Owens and Hahn, p. 174,175.
- 2003 *Paraphillipsia* – Jell and Adrain, p. 421,477.
- 2003 *Paraphillipsia* – Owens, p. 377,380,383,388,391.
- 2008 *Paraphillipsia* – Hahn and Hahn, p. 1,6,12,14,20,25,27,30,35,194,300–305,306,323.
- 2012 *Paraphillipsia* – Mychko, p. 575,577–580.
- 2016 *Paraphillipsia* – Mychko, p. 187–200.
- 2017 *Paraphillipsia* – Mychko and Alekseev, p. 67,68,69,70.
- 2019 *Paraphillipsia* – Schraut, p. 625–631.
- 2020 *Paraphillipsia* – Schraut, p. 217, tab. 3.
- Type species.** *Paraphillipsia karpinskyi* Tuman-skaya, 1935; Radian, Guadalupian; block of Dzhien-Sofu (=Totai-Koi), Salgir water pool, near of Simferopol City, Crimea; designated by Tuman-skaya (1935, p. 19).

Diagnosis. Cephalon elongated, rounded at genal angles; glabella large, swollen, long, “cummingellid” in shape (i.e., similar to that in *Cummingella*); L₁–lobes well defined, elongated towards occipital ring, separated by distinct S₁–furrows; furrows S₂–S₄ present, but very weakly expressed; eyes large, narrow, and bean-shaped; palpebral lobes shortened and protrude slightly to sides; facial sutures run close to glabella; thorax consists of 9 segments; pygidium semicircular, elongated in width; axis very wide, of moderate length, convex, and consists of 7–11 rings; lateral lobes convex, bearing up to nine pairs of pleural ribs (usually 5–6); no border furrow; surface of pygidium smooth.

Comparison (with Permian genera of the Cummingellinae). It differs from the closely related *Bedicella* Hahn and Hahn, 1990 in having smaller eyes, a longer pygidium, and the absence of a border furrow on it. It differs from *Cummingella* Reed, 1942 in the less pronounced S₂–S₄–furrows of the glabella, the L₁–lobes more elongated towards the occipital ring, the absence of a border furrow on the pygidium and a relatively wider axis.

Remarks. In a previous work (Mychko, 2012), the author reviewed the *Paraphillipsia* species described by Tumanskaya (1935) from the Guadalupian olistoliths of Crimea. According to the results of this study, the species *P. kussicum*, *P. netschaewi* and the variety *P. tauricum* var. *anfensis* were synonymized with the species *P. taurica*, since they do not have significant morphological differences from the latter. The authors of more recent studies agree with this opinion (e.g., Schraut, 2019).

Species. Eleven species and four species determined in open nomenclature (Table 2).

Occurrence. Cisuralian (Artinskian) – Lopingian (Changhsingian); Eurasia (Slovenia, Austria, Crimea, Tajikistan, China, Laos and Japan).

Paraphillipsia urushtensis sp. nov.

Figures 5A–J, 6F, G

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- 1944 *Paraphillipsia karpinskyi* – Weber, 1944, p. 12, pl. I, figs. 18–20, 22.
- 2003 *Paraphillipsia* aff. *karpinskyi* – Owens, 2003, Text-fig. 3 F,G.
- 2008 *Paraphillipsia karpinskyi* – Hahn and Hahn, 2008, Abb. 332–335.
- 2008 non *Paraphillipsia karpinskyi* – Hahn and Hahn, 2008, Abb. 331.

TABLE 2. Known species of *Paraphillipsia* Toumansky, 1930.

Species	Part	Stratigraphy	Geography
<i>P.?</i> <i>middlemissi</i> (Diener, 1897)	Py	Lopingian, Wuchiapingian (?), Chitichun Limestone	China, Tibet, Zanda County
<i>P.?</i> sp. (Mansuy, 1912)	Py	Guadalupian (?)	Laos, Ban Na Hai
<i>P. tschernyschewi</i> (Netschaew in Weber, 1932)	Cc, Cph	Cisuralian, Safetdaron Formation	Tajikistan, Darvaz, Safed-Daron village, Tangi-Gor Gorge
<i>P. pahara</i> Weller, 1935	Cr, Th, Py	Cisuralian (?), "reddish-gray coralline limestone"	China, Tibet, Eastern Karakoram, Chang Chenmo River valley
<i>P. karpinskyi</i> Tumanskaya, 1935	Cc	Guadalupian, Roadian	Crimea, the Dzhen-Sofu Block on the Salgir River
<i>P. baltensis</i> Tumanskaya, 1935	Py	Guadalupian, Roadian	Crimea, Kichkhi-Burnu Block on the Martha River
<i>P. taurica</i> Tumanskaya, 1935	Cr, Lg, Py	Guadalupian, Roadian	Crimea, Kichkhi-Burnu Block on the Martha River
<i>P. vnweberi</i> Tumanskaya, 1935	Cph, Py	Guadalupian, Roadian	Crimea, Kichkhi-Burnu Block on the Martha River
<i>P.?</i> sp. Weber, 1944	Py	Guadalupian, Capitanian, Chandalazian horizon	Far East, Partizanskaya River, Sen'kina Shapka Mountain
<i>P.?</i> sp., aff. <i>P.?</i> <i>taurica</i> Tumanskaya, 1935 (Hahn et Hahn in Hahn, Hahn et Ramovš, 1970)	Py	Cisuralian, Artinskian, Trogkofel Limestone	Slovenia, Karavanke, Dovžan Gorge
<i>P.?</i> sp. Hahn et Hahn, 1970	Py	Cisuralian, Artinskian, Trogkofel limestone	Slovenia, Karavanke, Dovžan Gorge
<i>P. levigata</i> Kobayashi et Hamada, 1980	Cr, Lg, Py	Guadalupian, Capitanian, Shimoyama Limestone, <i>Yabeina</i> zone	Japan, Shikoku, Sakawa
<i>P.?</i> <i>sinensis</i> Zhou, 1987	Cr, Th, Py	Cisuralian, Artinskian, Maping Formation	China, Guangxi Zhuang Autonomous Region, Bunuo
<i>P.?</i> <i>carnica</i> Schraut, 2019	Py	Cisuralian, Artinskian, upper part of Zottachkopf Formation	Austria, Carnic Alps, surroundings of the Trogkofel and Troghöhe Mountains
<i>P. urushtensis</i> sp. nov.	Cph, Cr, Py	Lopingian, Changhsingian, Belalabino Group	North Caucasus, Malaya Laba River Basin

2016 nomen nudum *Paraphillipsia urushtensis* – Mychko, 2016, p. 190–192, pl. III, figs. 3–6.

2017 *Paraphillipsia karpinskyi* – Mychko and Alekseev, p. 68.

Holotype. CNIGRmuseum, No. 62/5217, cephalon; Belalabino Group, Changhsingian, Lopingian; vicinity of the Urushten (outcrop No. 309), Malaya Laba River Basin Krasnodar Krai, Russia; selected here as the specimen with the best preservation.

Etymology. By the name of the Urushten.

Description. Cephalon oval, laterally flattened; wide glabella occupies majority of cephalon; glabella “cummingellid” in shape (has a constriction in the middle, and is slightly wider in the anterior part than in the posterior part); slightly swollen in front, descends steeply to anterior border, overlapping it; in posterior part of glabella long; barely noticeable L₁-lobes, quite wide, extending with their posterior

edges onto occipital ring; on some specimens the second glabellar furrows (S₂) barely visible; facial sutures very close to glabella; eyes large, long, bean-shaped, highly raised, occupying space from posterior end of librigena to anterior edge of glabella, where it bends towards border; palpebral lobes narrow; occipital ring long, narrow, with small median tubercle; librigenae steeply declined from glabella, with rounded genal angles; on surface of cephalon, especially glabella, very small tubercles visible, scattered in a checkerboard pattern; pygidium semicircular with broad axis bounded by distinct deep dorsal lateral furrows, gradually narrowing towards posterior edge; consists of nine clear rings; lateral lobes convex, with six pairs pleural ribs; interpleural furrows extend only to middle of lobes; pleural furrows indistinguishable; border furrow wide.

Dimensions (Tables 3, 4).

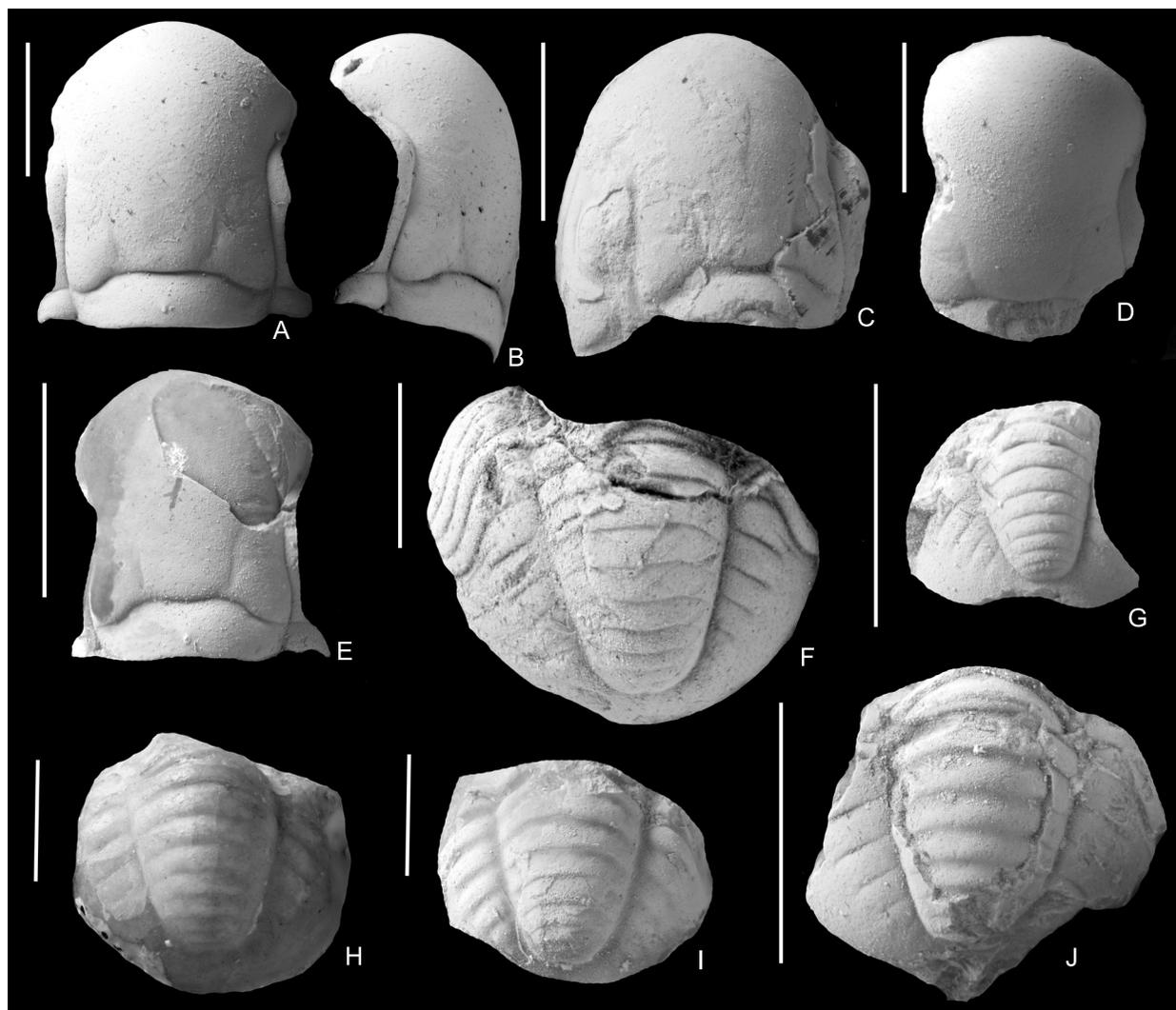


FIGURE 5. *Paraphillipsia urushtensis* sp. nov.; **A, B** – cranium, CNIGRMuseum, No. 61/5217; **C** – cephalon, CNIGRMuseum, No. 62/5217, holotype; **D** – cranium, CNIGRMuseum, No. 65/5217; **E** – cranium, CNIGRMuseum, No. 66/5217; **F** – pygidium with several pleura of thorax, CNIGRMuseum, No. 64/5217; **G** – pygidium, CNIGRMuseum, No. 68/5217; **H** – pygidium, CNIGRMuseum, No. 63/5217; **I** – pygidium, CNIGRMuseum, No. 67/5217; **J** – pygidium, CNIGRMuseum, No. 69/5217. Scale bars equal 5 mm.

Comparison. It is closest to *Paraphillipsia karpinskyi* (Figure 6A–E), but differs somewhat in the shape of the glabella: the median constriction at *P. urushtensis* is not as noticeable as in *P. karpinskyi*; L_1 -lobes of the former are somewhat larger than those of the latter and extend further onto the occipital ring. The eyes of *P. urushtensis* are narrower and longer, and librigenae of *P. karpinskyi* are wider. The pygidia both species are very similar, but the axis of *P. urushtensis* is comparatively longer, has a constriction, and does not taper as strongly towards the posterior as *P. karpinskyi*. The end of the axis at *P. karpinskyi* is more pointed than in *P. urushtensis*. Moreover, the axis of *P. urushten-*

sis consists of a smaller number of segments (in *P. karpinskyi* 10 axial rings are visible). As far as can be seen from the holotype of *P. karpinskyi*, the distance from the end of the axis to the edge of the pygidium at *P. urushtensis* is slightly less. It differs from *P. vnweberi* mainly in the morphology of the pygidium: which is wider, a shorter and narrower axis, more distinct interpleural furrows and more distinct furrows between the axial rings, as well as less segmentation of the axis (*P. vnweberi* has 10 rings and six pleural ribs). Also, the glabella of *P. vnweberi* has more obvious S_2 – S_3 pairs of furrows. It differs from *P. taurica* in less pronounced S_2 – S_4 pairs of glabellar furrows, the absence of an S_4

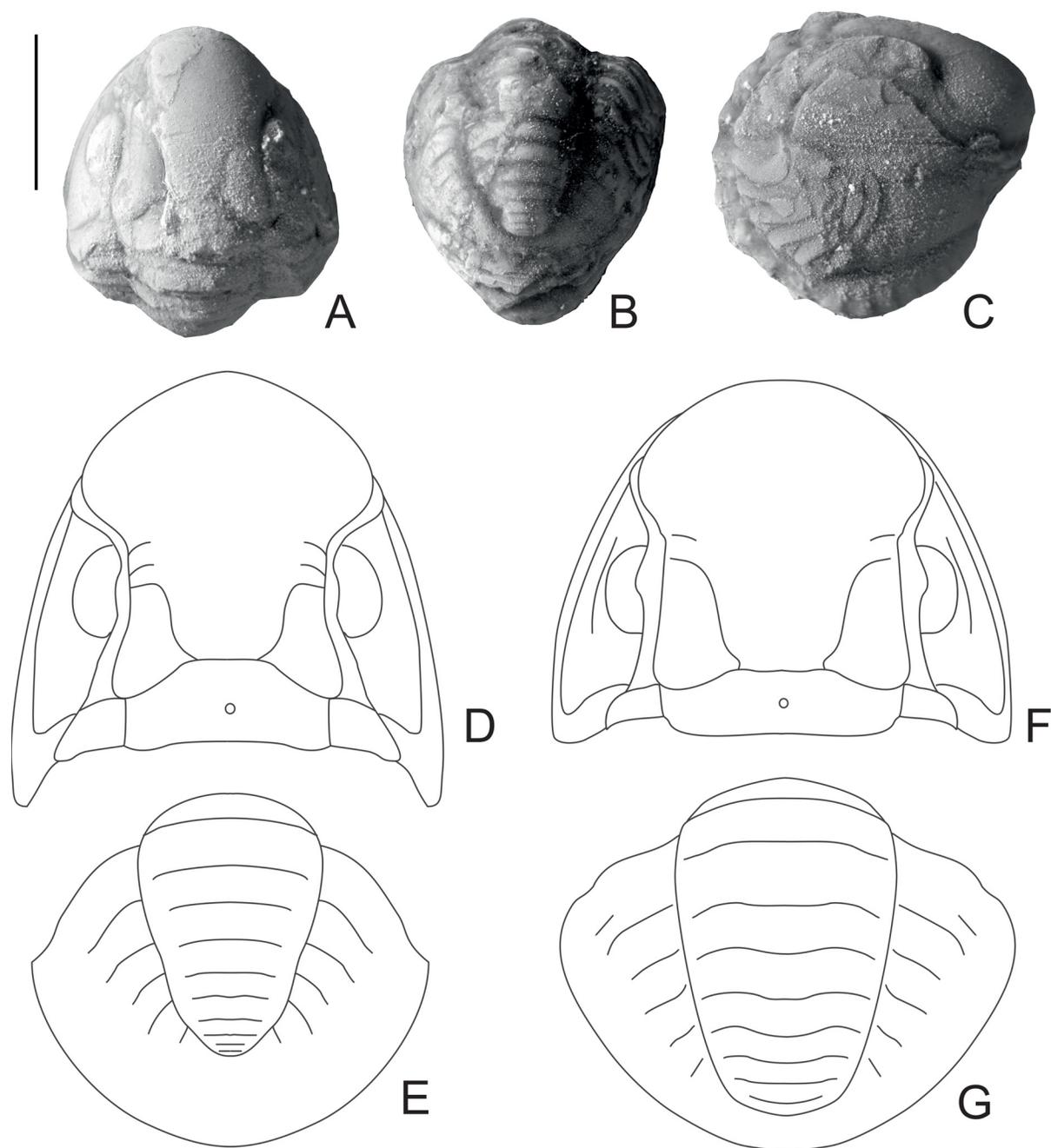


FIGURE 6. Comparison of *Paraphillipsia karpinskyi* Tumanskaya, 1935 (A–E) with *P. urushtensis* sp. nov. (F,G): **A–C** – complete enrolled exoskeleton, CNIGRMuseum, No. 59/9733, holotype; **D** – *P. karpinskyi* cephalon reconstruction; **E** – *P. karpinskyi* pygidium reconstruction; **F** – *P. urushtensis* cephalon reconstruction; **G** – *P. urushtensis* pygidium reconstruction. Scale bar equals 5 mm.

pair, a different shape of L_1 -lobes, the absence of obvious tuberculation on the exoskeleton, a smaller number of axial rings (*P. taurica* has 9–11 rings), a wider pygidium, a shortened axis, a smaller number of pleural ribs (*P. taurica* has 5–7 pairs of ribs) and shallower pleural furrows and furrows on between the axial rings. Pygidium of *P.*

urushtensis sp. nov. similar to *P. baltensis*, but differs in a large number of pleural ribs (the latter has only four pairs of noticeable ones). From *P. tschernyschewi* it differs a wider pygidium, an elongated axis, many axial rings (*P. tschernyschewi* has seven rings) and a large number of pleural ribs (*P. tschernyschewi* has three pairs of ribs). Compara-

TABLE 3. Dimensions (in mm) of the cephalon and crania of *Paraphillipsia urushtensis* sp. nov. LC – length of the cephalon, WC – width of the cephalon, LG – length of the glabella, LO – length of the occipital ring, WGA – width of the glabella at the anterior end, WGP – width of the glabella at the posterior end, LL – length of the L₁ lobes, LE – length of the eye.

Specimen	LC	WC	LG	LO	WGA	WGP	LL	LE
CNIGRMuseum, No. 62/5217	7.7	8.8	6.4	4.1	5.8	5.5	2.8	2
CNIGRMuseum, No. 61/5217	-	-	10.4	6.7	8	7	3.5	-
CNIGRMuseum, No. 65/5217	-	-	8.9	~5	8	6.9	3.1	-
CNIGRMuseum, No. 66/5217	-	-	6.4	4	5.1	4.4	2	-

TABLE 4. Dimensions (in mm) of pygidia of *Paraphillipsia urushtensis* sp. nov. LP – length of the pygidium, WP – width of the pygidium, WA – width of the axis at the anterior end, L/W – ratio of the length of the pygidium to its width, W/WA – ratio of the width of the pygidium to the width of the axis at the anterior end, DAB – distance from the end of the axis to edges of the border furrow of the pygidium.

Specimen	LP	WP	WA	L/W	W/WA	DAB
CNIGRMuseum, No. 63/5217	6.7	7.5	3.8	0.9	~2	1
CNIGRMuseum, No. 64/5217	7.5	9.6	5	0.8	~1.9	0.8
CNIGRMuseum, No. 67/5217	6.9	7.3	3.8	0.9	~1.9	0.6
CNIGRMuseum, No. 68/5217	~4	~4.4	2.3	0.9	~1.9	0.8
CNIGRMuseum, No. 69/5217	5.6	6.7	3.4	0.8	~2	>0.5
Average value	~6	~7	~3.7	~0.8	~1.9	0.8

tively *P. urushtensis* differs strongly from *P.? sinensis* in its glabella shape and less developed L₁-lobes. The pygidia are similar, but more elongated in length (the ratio of length to width of the pygidium in *P.? sinensis* is 0.7). Axis of *P.? sinensis* has fewer rings (7–8). It differs from *P. pahara* in having a more convex glabella, a less raised occipital ring, and also (apparently) in the presence of rudimentary of S₂-glabellar furrows, which are reduced in *P. pahara*. It differs greatly from *P. levigata* in the shape of the L₁-lobes, which are more elongated in the new species. The pygidium of *P. urushtensis* is distinguished by a smaller number of axial rings (in *P. levigata* there are 9–10) and pleural ribs (in *P. levigata* there are 7–8). It is similar to *P.? carnica* but differs in a smaller number of axial rings (the latter has 10 rings). From *P.? sp.*, described by Weber (1944, p. 12, pl. 1, fig. 21a,b), differs by a smaller number of axial rings and pleural ribs (Weber's species has >7 axial rings and most likely more than five pairs of ribs) and weaker interpleural furrows. From *P.? sp.*, aff. *P.? taurica*, described by Hahn and Hahn (1970), is different by a large number of axial rings (in *P.? aff. taurica* has seven axial rings). From another *P.? sp.*, also described by Hahn and Hahn (1970), differs in having the absence of an obvious border furrow (which, by the way, apparently may exclude the relation of this species to *Paraphillipsia*). It is rather difficult to

compare with *P. middlemissi*, since we only have a drawing (Diener, 1897, pl. I, fig. 3a–b), but the number of axial rings and pleural ribs correspond to those of *P. urushtensis* sp. nov.

Remarks. Despite minor differences in morphology between *Paraphillipsia karpinskyi* and *P. urushtensis* sp. nov. I cannot attribute them to the same species, since the deposits from which their type series originate represent different stratigraphic intervals (the Roadian of the Guadalupian and the Changhsingian of the Lopingian). The interval between the formation of these deposits and the existence of these species is about or more than 10 Ma. More likely, *P. urushtensis* sp. nov. is a close relative descended from *P. karpinskyi*. It is worth noting that we do not have complete exoskeletons of *P. urushtensis* sp. nov., and we cannot with full confidence attribute the discussed pygidia (Table 5) to this species.

Occurrence. Lopingian, Changhsingian; Russia (Krasnodar Krai, North Caucasus, Malaya Laba River Basin).

Material. Nine specimens (Table 5).

Subfamily BOLLANDIINAE Hahn and
Brauckmann, 1988
Genus KATHWAIA Grant, 1966

1966 *Kathwaia* – Grant, p. 69–71.

TABLE 5. Type series of *Paraphillipsia urushtensis* sp. nov.

Number of specimens	Part	Locality	Author of find, year	Photos
CNIGRMuseum, No. 61/5217	Cr	Urushten tract (=paraje), outcrop No. 309	V.N. Robinson, 1925	Weber, 1944, pl. I, fig. 18; Hahn and Hahn, 2008, Abb. 333; Mychko, 2016, pl. III, fig. 6; herein – Figure 5 A, B
CNIGRMuseum, No. 62/5217	Cph	3 km from the estuary of the Urushten River, outcrop No. 265	V.N. Robinson	Weber, 1944, pl. I, fig. 22; Hahn and Hahn, 2008, Abb. 332; Mychko, 2016, pl. III, fig. 3; herein – Figure 5 C
CNIGRMuseum, No. 63/5217	Py	3,5 km from the estuary of the Urushten River, outcrop No. 27	B.K. Likharev, 1927	Weber, 1944, pl. I, fig. 19; Hahn and Hahn, 2008, Abb. 334 a, b; Mychko, 2016, pl. III, fig. 5; herein – Figure 5 H
CNIGRMuseum, No. 64/5217	Py	3 km from the estuary of the Urushten River, outcrop No. 263	V.N. Robinson	Weber, 1944, pl. I, fig. 20; Hahn and Hahn, 2008, Abb. 335; Mychko, 2016, pl. III, fig. 4; herein – Figure 5 F
CNIGRMuseum, No. 65/5217	Cr	3 km from the estuary of the Urushten River, outcrop No. 263	V.N. Robinson	herein – Figure 5 D
CNIGRMuseum, No. 66/5217	Cr	3,5 km from the estuary of the Urushten River, outcrop No. 27	B.K. Likharev, 1927	herein – Figure 5 E
CNIGRMuseum, No. 67/5217	Py	3,5 km from the estuary of the Urushten River, outcrop No. 27	B.K. Likharev, 1927	herein – Figure 5 I
CNIGRMuseum, No. 68/5217	Py	3,5 km from the estuary of the Urushten River, outcrop No. 27	B.K. Likharev, 1927	herein – Figure 5 G
CNIGRMuseum, No. 69/5217	Py	2,25 from the estuary of the stream in Nikitinskaya Ravine	B.K. Likharev, 1927	herein – Figure 5 J

1967 *Kathwaia* – Hahn and Hahn, p. 336, 337, 343, 345, 346.

1970 *Kathwaia* – Hahn and Hahn, p. 231.

1975 *Kathwaia* – Hahn and Hahn, p. 16, 17, 61.

1980 *Kathwaia* – Haas, Hahn, and Hahn, tab. 8.

1983 *Kathwaia* – Owens, p. 16, 17, 36, 37.

1984 *Kathwaia* – Hahn, Hahn, and Brauckmann, p. 66, 67.

1984a *Kathwaia* – Kobayashi and Hamada, p. 23, 25, 28, 84.

1985 *Kathwaia* – Kobayashi and Hamada, p. 282.

1988 *Kathwaia* – Hahn and Brauckmann, p. 121, 126.

1989b *Kathwaia* – Hahn, Hahn, and Yuan, p. 174, 175.

1992 *Kathawaia* [sic!] – Brezinski, p. 927.

1993 *Kathwaia* – Owens and Hahn, p. 174, 175.

2001 *Kathwaia* – Hahn, Hahn, and Brauckmann, p. 271, 272, 274.

2003 *Kathwaia* – Jell and Adrain, p. 391, 477.

2003 *Kathwaia* – Owens, p. 380, 386, 388, 391.

2012 *Kathwaia* – Lerosey-Aubril and Feist, p. 551.

2015 *Kathwaia* – Hahn and Hahn, p. 3, 6, 11, 15, 18, 19, 20, 103–104, 109.

2016 *Kathwaia* – Mychko, 2016, p. 38, 178–181.

Types species. *Kathwaia capitorosa* Grant, 1966 (= *K. caucasica* (Weber, 1944)); Lopingian; Pakistan (Kathwai–Kushab, Salt Range) and Russia (Malaya Laba River Basin, Krasnodar Krai).

Diagnosis. Cephalon subtriangular, semi-elliptical; glabella strongly swollen, hangs vertically and overlaps anterior border; large, separate and distinct L₁-lobes; fixigenae narrow; small eyes sickle-shaped; sculpture often represented by large tubercles scattered; pygidium elongated; pygidial axis consists of 7–9 rings, lateral lobes have 6–9

TABLE 6. Known species of *Kathwaia* Grant, 1966 adopted in this work.

Species	Part	Stratigraphy	Geography
<i>K. girtyi</i> (Tumanskaya, 1935)	Th, Py	Guadalupian, Roadian	Crimea, Kichkhi-Burnu Block on the Martha River
<i>K. (?) sinensis</i> (Grabau, 1936)	Cc	Upper Pennsylvanian or Cisuralian, Maping Formation	China, Guangxi Zhuang Autonomous Region
<i>K. caucasica</i> (Weber, 1944) (including <i>K. capitorosa</i> Grant, 1966)	Cc, Cph, Cr, Gl, Py	Lopingian, Wuchiapingian – Changhsingian	Krasnodar Krai, Malaya Laba River Basin and Pakistan (Salt Range, Kathwai–Kushab)
<i>K.? kashmirensis</i> (Sarkar 1968)	Py	Cisuralian (?)	India, Kashmir, vicinity of the Aishmuquam
<i>K.? sp.</i> König et Kuss, 1980	Cc	Cisuralian, Talea Ori Group	Greece, Crete, Bali village

pairs of pleural ribs; pleural ribs ornamented with two rows of tubercular.

Comparison. The genus is similar to *Bollandia* Reed, 1943 but differs in reduced S_2 – S_4 pairs of glabellar furrows, more distinct L_1 –lobes, smaller eyes and palpebral lobes, and the presence of tubercle ornamentation on the exoskeleton. It differs from *Neoproetus* Tesch, 1923 in having distinct and more distinct L_1 –lobes, deeper and wider S_1 –furrows, the absence of a wrinkled structure on the surface of the glabella, and the presence of numerous tubercles on the exoskeleton. It differs from *Neogriffithides* Toumanský, 1930 in reduced S_2 – S_4 –pairs of glabellar furrows, more isolated L_1 –lobes, stronger and coarser tuberculation of the cephalon and pygidium, and smaller eyes. It differs from *Carbonoproetus* Gandl, 1987 in the shape of the glabella which is closer to conical and flatter, reduced S_2 – S_4 –pairs of glabellar furrows, and more isolated L_1 –lobes. It differs from *Reediella* Osmólska, 1970 in the shape of the glabella, which is closer to conical and less swollen, reduced S_2 – S_4 –pairs of glabellar furrows (in *Reediella* the S_2 and S_3 pairs are highly developed), more isolated L_1 –lobes, and less segmentation of the pygidium.

Species. Four species and one species determined in open nomenclature (Table 6).

Occurrence. Cisuralian (?) – Lopingian (Changhsingian); Crimea and North Caucasus, Greece (?), India (?), China (?) and Pakistan.

	<i>Kathwaia caucasica</i> (Weber, 1944) Figures 7A–K, 8A–H		
1932	nomen nudum <i>Proetus? semipustulatus</i> – Weber in Robinson, p. 23.	2003	<i>Kathwaia capitorosa</i> – Owens, p. 380, text-fig. 3 A–B.
1944	<i>Proetus (?) girtyi caucasica</i> – Weber, p. 15, pl. II, figs. 16, 17.	2015	<i>Kathwaia caucasica</i> – Hahn and Hahn, p. 106–107, Abb. 110.
		1944	<i>Griffithides (Neogriffithides) cf. almensis</i> – Weber, p. 11, pl. I, figs. 15, 16.
		1966	<i>Kathwaia capitorosa</i> – Grant, p. 71–72, pl. 13, fig. 1 a–d.
		1970	<i>Kathwaia capitorosa</i> – Hahn and Hahn, p. 231.
		1970	<i>Kathwaia sp.</i> – Hahn and Hahn, p. 233.
		1970	<i>Kathwaia girtyi caucasica</i> – Hahn and Hahn, p. 232.
		1970	<i>Kathwaia sp.</i> – Hahn and Hahn, p. 233.
		1975	<i>Kathwaia capitorosa</i> – Hahn and Hahn, p. 17, 61, pl. 12, fig. 1 a–b.
		1983	<i>Kathwaia capitorosa</i> – Owens, p. 17, pl. 2, figs. 1–4.
		1983	<i>Proetus (?) girtyi</i> – Owens, p. 17.
		1983	<i>Griffithides (Neogriffithides) cf. almensis</i> – Owens, p. 17.
		1984a	<i>Kathwaia capitorosa</i> – Kobayashi and Hamada, p. 22, 29.
		1984a	<i>Kathwaia girtyi caucasica</i> – Kobayashi and Hamada, p. 25.
		1987	<i>Kathwaia capitorosa</i> – Kobayashi and Hamada, p. 141.
		1988	<i>Kathwaia capitorosa</i> – Hahn and Brauckmann, pl. 2, figs. 20–21.
		1989b	<i>Kathwaia capitorosa</i> – Hahn, Hahn, and Yuan, 153.
		2001	<i>Kathwaia capitorosa</i> – Hahn, Hahn, and Brauckmann, p. 275, 276, 294, pl. 2, fig. 1 a–d.
		2003	<i>Kathwaia capitorosa</i> – Jell and Adrain, p. 391.

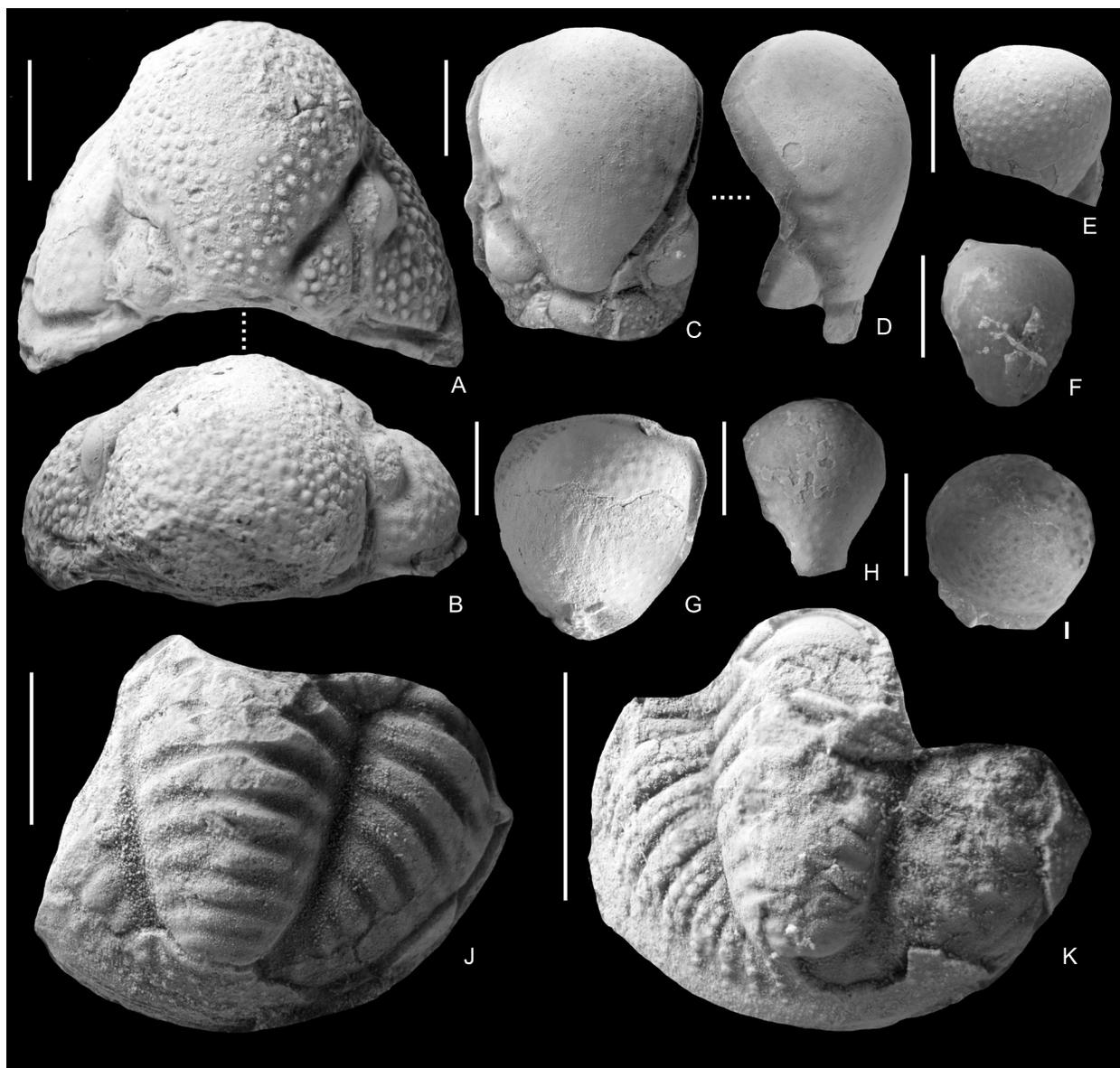


FIGURE 7. *Kathwaia caucasica* (Weber, 1944); **A,B** – cephalon, CNIGRMuseum, No. 53/5217; **C,D** – cranium (cast), CNIGRMuseum, No. 54/5217; **E** – incomplete glabella (cast), CNIGRMuseum, No. 55/5217; **F** – glabella (cast), CNIGRMuseum, No. 58/5217; **G** – incomplete glabella (cast), CNIGRMuseum, No. 57/5217; **H** – glabella (cast), CNIGRMuseum, No. 56/5217; **I** – incomplete glabella (cast), CNIGRMuseum, No. 59/5217; **J** – incomplete pygidium (cast with a fragment of exoskeleton), CNIGRMuseum, No. 87/5217; **K** – incomplete pygidium, CNIGRMuseum, No. 88/5217, lectotype. Scale bars equal 5 mm.

2015 *Kathwaia capitorosa* – Hahn and Hahn, p. 6, 9, 103, 104–106, 107, Abb. 108–109.

2016 *Kathwaia caucasica* – Mychko, p. 180–181, pl. II, figs. 17–20.

2017 *Proetus girtyi* var. *caucasica* – Mychko and Alekseev, p. 68.

Lectotype. CNIGRMuseum, No. 88/5217, incomplete pygidium; Lopingian, Changhsingian, Urushten Formation; Russia, Krasnodar Krai, Malaya

Laba River Basin, vicinity of the Urushten; designated by Hahn and Hahn (1970, p. 232).

Paralectotype. CNIGRMuseum, No. 53/5217, cephalon; Lopingian, Changhsingian, Urushten Formation; Russia, Krasnodar Krai, Malaya Laba River Basin, Gefo Mountain, blocks along the Tegen' River, outcrop No. 30; designated here.

Hypotype. USNM PAL 145320, complete enrolled exoskeleton; Lopingian, Wuchiapingian, Wargal

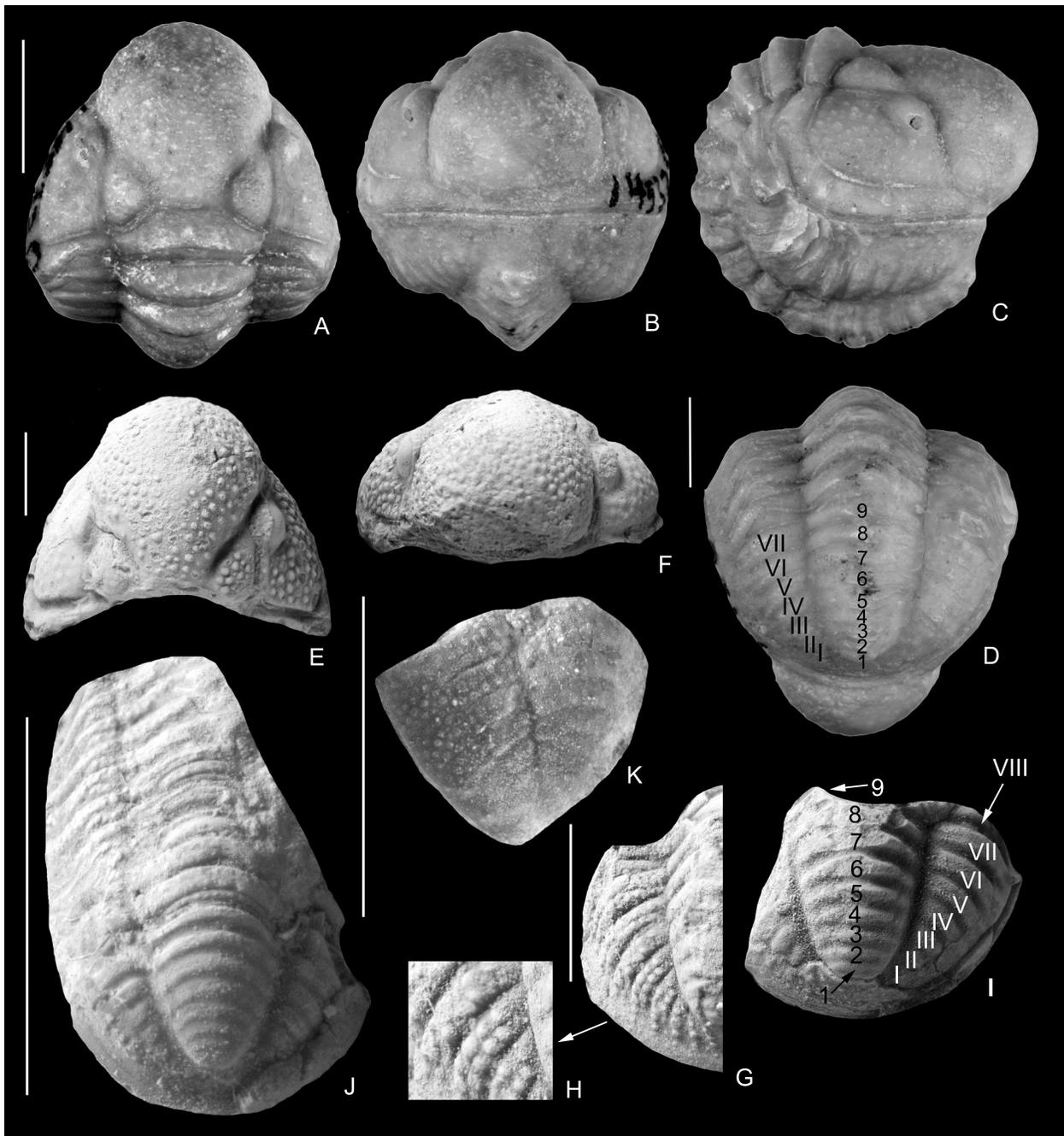


FIGURE 8. Members of *Kathwaia* Grant, 1966; **A–K** – *K. caucasica* (Weber, 1944): **A–D** – complete enrolled exoskeleton, USNM PAL, No. 145320, Lopingian, Wuchiapingian, Pakistan, Salt Range, Kathwai–Kushab, holotype of *K. capitorosa* Grant, 1966 (junior subjective synonym of *K. caucasica*); **E, F** – cephalon, CNIGRMuseum, No. 53/5217; **G, H** – pygidium, CNIGRMuseum, No. 87/5217, general view, left half (**G**) and an enlarged fragment of pleural ribs with rows of tubercles (**H**); **I** – pygidium, CNIGRMuseum, No. 87/5217; **J, K** – *K. girtyi* (Tumanskaya, 1935), Guadalupian, Roadian; Crimea, Martha River, Kichkhi-Burnu Block; **J** – thorax with pygidium, CNIGRMuseum, No. 137/9733; **K** – pygidium, CNIGRMuseum, No. 139/9733. Roman numerals refer to pleural ribs, while Arabic numerals denote axial rings. Scale bars equal 5 mm.

Formation (=Wargal Limestone or Middle *Productus* Limestone); Pakistan, Salt Range, Kathwai–Kushab; holotype of *Kathwaia capitorosa* Grant, 1966.

Description. Cephalon elongated; glabella strongly swollen, hangs vertically and overlaps narrow and convex anterior border; L_1 –lobes distinct, large, subtriangular, separated by deep S_1 –furrows; S_2 – S_4 –furrows not noticeable (but on casts above L_1 –lobes, in middle part of glabella, three pairs of small swellings, which obviously L_2 – L_4 –lobes); occipital ring relatively narrow, with median tubercle; fixigenae very narrow, as facial sutures located close to dorsal furrows; palpebral lobes small and do not completely cover visual surfaces of eyes; eyes small, smaller than L_1 –lobes; librigenae convex and have deep border furrow, sharply separating lateral border; cephalon ends at rounded genal angles; surface of cephalon, except for anterior border, covered with large, closely spaced tubercles of same size; anterior border with terrace lines; thorax consists of nine segments; on dorsal side of axial rings row of small tubercles; pygidium relatively large, elongated and semi-elliptical; axis subtriangular-rounded in cross-section,

strongly convex, shortened and relatively wide: the ratio of width of pygidium to width of axis in anterior part – 2:4; it tapers slightly towards posterior end, where it terminates bluntly, not reaching pygidial border; it has nine rings separated by deep furrows; lateral lobes slightly convex; they contain 7–8 pairs of pleural, distinct ribs, separated by deep interpleural furrows; pleural ribs with slight backward bend; pleural furrows distinct, dividing pleural ribs into two parts equal in width; ribs with two rows of large tubercles (from five to 10); border furrow absent and pleural ribs merge into pygidial border, ornamented with thin terrace lines.

Dimensions (Tables 7, 8).

Comparison. Very similar to *Kathwaia girtyi* (Figure 8J, K), but differs in relatively larger sizes (pygidia of *K. girtyi* are less than 3 mm wide), a different shape of the axis (in *K. girtyi* it is shorter and tapers more strongly towards the posterior end), a large number of axial rings and pleural ribs (*K. girtyi* has about eight rings and six pairs of pleural ribs), as well as a smaller number of larger, densely located tubercles on the pleural ribs. It differs from *K. sinensis* in the less pronounced tuber-

TABLE 7. Dimensions (in mm) of cephalae, cranidia and glabellae of *Kathwaia caucasica* (Weber, 1944). LC – length of the cephalon, WC – width of the cephalon, LG – length of the glabella, LO – length of the occipital ring, WGA – width of the glabella at the anterior part, WGP – width of the glabella at the posterior part, LL – length of the L_1 lobes, LE – length of the eye.

Specimen	LC	WC	LG	LO	WGA	WGP	LL	LE
CNIGRMuseum, No. 53/5217	~12	16.9	10.2	~5.8	9.2	3.5	4	2.8
USNM PAL 145320	8.5	11.7	6.7	5.6	6.2	2.6	2.7	1.5
CNIGRMuseum, No. 54/5217	-	-	13.5	~8	10.9	4.7	4.3	-
CNIGRMuseum, No. 55/5217	-	-	-	-	12.6	-	-	-
CNIGRMuseum, No. 56/5217	-	-	9.2	-	7.4	2.6	-	-
CNIGRMuseum, No. 57/5217	-	-	11.5	-	10	4.6	-	-
CNIGRMuseum, No. 58/5217	-	-	~9	-	7	~3.5	-	-
CNIGRMuseum, No. 59/5217	-	-	8	-	6.3	3	-	-
Average value	10.3	14.3	9.73	6.5	8.7	3.5	3.7	2.2

TABLE 8. Dimensions (in mm) of pygidia of *Kathwaia caucasica* (Weber, 1944). LP – length of the pygidium, WP – width of the pygidium, WA – width of the axis at the anterior end, L/W – ratio of the length of the pygidium to its width, W/WA – ratio of the width of the pygidium to the width of the axis at the anterior end, DAB – distance from the end of the axis to edges of the border furrow of the pygidium.

Specimen	LP	WP	WA	L/W	W/WA	DAB
CNIGRMuseum, No. 87/5217	12	~17	8	0.7	2.1	2
CNIGRMuseum, No. 88/5217	8	11.3	4.3	0.7	2.6	1.4
USNM PAL 145320	7.9	11.3	4.5	0.7	2.5	1
Average value	9.3	13.2	5.6	0.7	2.4	1.5

ulation of the cranidium, smaller L_1 -lobes and a more convex glabella.

Remarks. Part of the type series of the species under discussion (pygidia, specimen CNIGRMuseum, No. 87 and 88/5217) were first described by Weber (1944, p. 15) as a subspecies *Proetus* (?) *girtyi* var. *caucasica*. By that time, the cephalia (CNIGRMuseum, No. 53–59/5217) were provisionally attributed to Weber (1944, p. 11) to another species *Griffithides* (*Neogriffithides*) cf. *almensis*.

Later pygidia *Proetus* (?) *girtyi* var. *caucasica* and cephalia *Griffithides* (*Neogriffithides*) cf. *almensis* were described by Hahn and Hahn (1970, pp. 232–233) as *Kathwaia girtyi caucasica* and *Kathwaia* sp. respectively. And in a newer revision (Hahn and Hahn, 2015), the subspecies *Kathwaia girtyi caucasica* was identified as an independent species *Kathwaia caucasica*, and the cephalia of *Kathwaia* sp. (= *Griffithides* (*Neogriffithides*) cf. *almensis*) were assigned to *Kathwaia capitorosa*.

Since both pygidia and cephalia come from coeval deposits of the North Caucasus, I believe that they most likely belong to the same species.

Moreover, the identical morphology of cephalia from the Changhsingian of the North Caucasus with that of the Pakistani *Kathwaia capitorosa* allows us to consider the latter a junior synonym of *Kathwaia caucasica*. Small differences in the pygidium (North Caucasian pygidia have one more pair of pleural ribs) can be considered as intraspecific variability due to insufficient material.

It is worth noting that on some glabella moulds (Figure 7C, D, H) small, faintly defined lobes L_2 – L_4 visible. However, these are not observed on specimens with an exoskeleton. The absence of lobes on the glabella (except L_1) is one of the main diagnostic characters of *Kathwaia*. Apparently, we are observing an incompletely reduced trait inherited from ancestral forms (Hahn and Hahn, 2015, Abb. 4), such as the Mississippian genus *Bollandia*.

Occurrence. Lopingian, Wuchiapingian–Changhsingian; Russia (Krasnodar Krai, North Caucasus) and Pakistan.

Material. 10 specimens (Table 9).

TABLE 9. Hypodygm (type series and hypotype) of *Kathwaia caucasica* (Weber, 1944).

Number	Part	Locality	Author of finding, year	Photo
CNIGRMuseum, No. 87/5217	Py	Raskol-Skala Mountain, near Khamyshki Village, western part of the block, outcrop No. 42	B.K. Likharev, 1927	Weber, 1944, pl. II, fig. 16; Mychko, 2016, pl. II, fig. 17; herein – Figure 7 J
CNIGRMuseum, No. 88/5217	Py	3 km from Urushten tract (=paraje), outcrop No. 264	V.N. Robinson	Weber, 1944, pl. II, fig. 17; Hahn and Hahn, 2015, abb. 110; Mychko, 2016, pl. II, fig. 18; herein – Figure 7 K
CNIGRMuseum, No. 53/5217	Cph	Gefo Mountain, blocks along the Tegen' River, outcrop No. 30	B.K. Likharev, 1927	Weber, 1944, pl. I, fig. 15; Hahn and Hahn, 2015, abb. 109; Mychko, 2016, pl. I, fig. 20; herein – Figure 7 A, B
CNIGRMuseum, No. 54/5217	Cr	Raskol-Skala Mountain, near Khamyshki Village, western part of the block, outcrop No. 42	B.K. Likharev, 1927	Weber, 1944, pl. I, fig. 16; Mychko, 2016, pl. I, fig. 19; herein – Figure 7 C, D
CNIGRMuseum, No. 55/5217	Gl	- // -	- // -	herein – Figure 7 E
CNIGRMuseum, No. 56/5217	Gl	- // -	- // -	herein – Figure 7 H
CNIGRMuseum, No. 57/5217	Gl	- // -	- // -	herein – Figure 7 G
CNIGRMuseum, No. 58/5217	Gl	- // -	- // -	herein – Figure 7 F
CNIGRMuseum, No. 59/5217	Gl	- // -	- // -	herein – Figure 7 I
USNM PAL 145320	Cc	Pakistan, Salt Range, near the Kathwai Village	A.N. Fatmi, 1963–1964	Grant, 1966, pl. 13, fig. 1a–d; Owens, 1983, pl. 2, fig. 1–4; Hahn and Brauckmann, 1988, Taf. 2, fig. 20–21; Owens, 2003, text-fig. 3A–B; Hahn and Hahn, 2015, Abb. 108–109; herein – Figure 8 A–D

- Subfamily DITOMOPYGINAE Hupé, 1953
Genus PSEUDOPHILLIPSIA Gemmellaro, 1892
- 1892 *Pseudophillipsia* – Gemmellaro, p. 21.
1930 *Pseudophillipsia* – Toumansky, 1930, p. 474,477.
1933 *Griffithides (Pseudophillipsia)* – Weber, 1933, p. 9,10,12–17,46–48,57.
1935 *Pseudophillipsia* – Tumanskaya, 1935, p. 24–25.
1935 *Pseudophillipsia* – Weller, p. 34.
1937 *Griffithides (Pseudophillipsia)* – Gheyselincx, 1937, p. 49, 50, 51, 53–55,59.
1939 *Pseudophillipsia* – Licharew, p. 198.
1944 *Pseudophillipsia* – Teichert, p. 457–458.
1944 *Pseudophillipsia* – Weber, p. 5–6.
1944 *Pseudophillipsia* – Weller, p. 324–325.
1955 *Pseudophillipsia* – Hupé, p. 210.
1957 *Pseudophillipsia* – Goldring, p. 197–201, 201–202.
1959 *Pseudophillipsia* – Weller, p. 0402–403.
1960 *Pseudophillipsia* – Maximova, p. 140.
1970 *Pseudophillipsia* – Hahn, Hahn, and Ramovš, p. 314.
1970 *Pseudophillipsia* – Hahn and Hahn, p. 165, 303–304.
1974 *Pseudophillipsia* – Termier and Termier, p. 260.
1975 *Pseudophillipsia* – Hahn and Hahn, p. 15,17, 67, 83.
1975 *Pseudophillipsia (Pseudophillipsia)* – Hahn and Brauckmann, p. 119;
1977 *Pseudophillipsia* – Qian, 1977, p. 279–280.
1983 *Pseudophillipsia* – Owens, p. 28–29.
1984a *Pseudophillipsia (Pseudophillipsia)* – Kobayashi and Hamada, p. 17, 20,51, 52, 56.
1984a *Pseudophillipsia (Nodiphillipsia)* – Kobayashi and Hamada, p. 9,15,16, 20, 51, 52, 58, 83.
1993 *Pseudophillipsia (Nodiphillipsia)* – Owens and Hahn, p. 174.
1998 *Pseudophillipsia (Nodiphillipsia)* – Ishibashi, p. 226.
2001 *Pseudophillipsia (Pseudophillipsia)* – Hahn, Hahn, and Brauckmann, p. 272–273.
2001 *Pseudophillipsia (Nodiphillipsia)* – Hahn, Hahn, and Brauckmann, p. 273–274.
2003 *Pseudophillipsia* – Owens, p. 382, 385, 388.
2003 *Pseudophillipsia* – Jell and Adrain, p. 434,477.
2003 *Nodiphillipsia* – Jell and Adrain, p. 412,477.
2009 *Pseudophillipsia (Nodiphillipsia)* – Lerosey-Aubril and Angiolini, p. 433–438.
2011 *Pseudophillipsia (Pseudophillipsia)* – Gandl, p. 95–98.
2012 *Pseudophillipsia* – Lerosey-Aubril, p. 10.
2015 *Pseudophillipsia (Nodiphillipsia)* – Fortey and Heward, p. 208.
2016 *Pseudophillipsia (Pseudophillipsia)* – Mychko, p. 46, 253–254.
2016 *Pseudophillipsia (Nodiphillipsia)* – Mychko, p. 47,61, 253.
2020 *Pseudophillipsia (Nodiphillipsia)* – Schraut, p. 214.
2021 *Pseudophillipsia (Nodiphillipsia)* – Flick and Shiino, p. 117.
- Type species.** *Phillipsia sumatrensis* Roemer, 1880; Guadalupian, Wordian; Indonesia, Sumatra; designated by Hahn and Brauckmann (1975, p. 118).
- Diagnosis.** Exoskeleton elongated; cephalon semi-elliptical in outline, ending in medium or long genal spines; in some species latter may have a spatulate shape; eyes medium to large, bean-shaped; behind glabella lateral and unpaired (medial) preoccipital lobes; in posterior part of glabella distinctive “festoon structure” formed by three pairs of L₂–L₄, typically these convex, well separated, and semicircular; surface of glabella, apart from lobes, usually smooth; number of thoracic segments – 9; pygidium elongated, oval-triangular; pygidial axis has ~20–27 rings separated by distinct furrows and has lateral constriction; pleural ribs – 10–17.
- Comparison.** From the closely related subgenus *Ditomopyge (Carniphillipsia)* is differs by the presence of a “festoon structure” in the posterior part of the glabella, formed by isolated L₂–L₄ lobes, and also, sometimes, by a larger number of axial rings at pygidium. It differs from *Acropyge* in the less triangular pygidium and the absence of a post-axial ridge behind the axis. Similar to *Anisopyge*, but differs in a different shape of the glabella, more isolated preoccipital lobes, a less triangular shape of the pygidium, and a smaller number of axial rings (in the latter their number reaches 33).

Discussion. Members of *Pseudophillipsia* are characterized mainly by the presence of a so-called “festoon structure” in the posterior part of the glabella, formed by the lobes L_2 – L_4 . This character, as well as the highly segmented pygidium, have long been the main distinguishing characters of this genus from other members of the subfamily Ditomopyginae, in particular the nominative genus *Ditomopyge*, widespread in the Late Pennsylvanian and Cisuralian and surviving until the Lopingian.

In 1965, Gauri (1965) described several *Pseudophillipsia* species from the Upper Pennsylvanian of the Carnic Alps (Austria), particularly *Pseudophillipsia ogivalis*, which has a highly segmented pygidium (18+ axial rings and 10 pleural ribs). However, glabella of *Ps. ogivalis* does not have L_2 – L_4 –lobes, which makes it more similar to *Ditomopyge*. Gauri noted (1965, p. 13) that the species he identified appears to be a transitional form between the earlier genus *Ditomopyge* and the later *Pseudophillipsia*.

Later, Hahn and Brauckmann (1975) divided the genus *Pseudophillipsia* into two subgenera: *Ps. (Pseudophillipsia)* and *Ps. (Carniphillipsia)*. Type species of the latter subgenus is *Ps. ogivalis*. They noted that the anterior glabellar furrows (S_2 – S_4) at *Ps. (Carniphillipsia)* weakly incised or absent, but preoccipital (lateral and medial) lobes very distinct. In their opinion, the pygidia of *Ps. (Pseudophillipsia)* and *Ps. (Carniphillipsia)* differed in the degree of segmentation: *Ps. (Pseudophillipsia)* – has 20–27 axial rings and 13–17 pleural ribs, at *Ps. (Carniphillipsia)* – 17–21 axial rings and 9–13 pleural ribs.

That *Carniphillipsia* can be considered a subgenus of both *Pseudophillipsia* and *Ditomopyge* has been noted previously (e.g., Owens, 1983, p. 28). Gandl (2011, p. 72) made a detailed argument for *Carniphillipsia* is a subgenus of *Ditomopyge*. Both the author of this work, and recent publications (Mychko and Alekseev, 2018), and other authors (e.g., Schraut, 2020, p. 211) agree with this opinion.

The differences between *Ditomopyge (Carniphillipsia)* and *Pseudophillipsia* can only be observed in the structure of the cephalon; the pygidia of both taxa cannot serve as a reliable element for identification. Despite the opinion that the pygidia of *Ditomopyge (Carniphillipsia)* are less segmented than those of *Pseudophillipsia*, which is given in various works (e.g., Hahn and Brauckmann, 1975; Kobayashi and Hamada, 1984a), there are species among *Ditomopyge (Carniphillip-*

sia), which may even have 22–25 axial rings and up to 15 pairs of pleural ribs. This high degree of segmentation of the pygidium is quite consistent with that of *Pseudophillipsia*.

This raises the fundamental and important problem of identifying Permian trilobites solely from pygidia. Previously, researchers, having no remains of cranidia, classified one or another highly segmented pygidium as *Pseudophillipsia* in the broad sense (sensu lato). A similar record – *Pseudophillipsia* (s.l.) – can be seen, for example, in the work of Lerosey-Aubril (2012), which meant that the pygidium under study can be attributed to any of the subgenera of *Pseudophillipsia*. However, if we adhere to the opinion that *Carniphillipsia* belongs to the genus *Ditomopyge*, such a record becomes inappropriate. Therefore, I propose to classify species and species determined in open nomenclature known only from pygidia into the genus *Pseudophillipsia* conditionally, with a question mark. In some ways, *Pseudophillipsia* becomes a “junk taxon”, which includes representatives of *Ditomopyge (Carniphillipsia)*, for which the cephalon is unknown. But this is a temporary solution until reliable new discoveries of cephalons are made.

Almost 10 years after the description of *Pseudophillipsia (Carniphillipsia)*, Kobayashi and Hamada (1984b) described another subgenus of *Pseudophillipsia* – *Ps. (Nodiphillipsia)*. Type species of this, *Ps. (Nodiphillipsia) spatulifera* from the Guadalupian of Japan. According to the authors, the only and most important difference between the new subgenus and *Ps. (Pseudophillipsia)* was what *Ps. (Nodiphillipsia) L_2–L_4–lobes of the glabella were small swollen nodules. The number of axial rings (23) and pleural ribs (17–18) at *spatulifera* was quite consistent with that in representatives of *Pseudophillipsia*. It is interesting that in *Ps. (Nodiphillipsia)* Kobayashi and Hamada classified a number of species, including described in this article *Ps. solida*.*

However, Kobayashi and Hamada did not take into account that the type material of all species they classified as *Pseudophillipsia (Nodiphillipsia)* is represented by casts. And the lobes of the glabella, which appear to be knots or nodules, are only the result of conservation. This was noted by Hahn, Hahn and Brauckmann (2001, p. 273). It was clarified that the type species, *Ps. (Nodiphillipsia) spatulifera* has special (highly specialized) spatulate-shaped genal spines, which are unusual for other representatives of *Pseudophillipsia*.

This feature made it possible to retain *Pseudophillipsia* (*Nodiphillipsia*) in the work of Lerosey-Aubril and Angiolini (2009), where the authors clarified the diagnosis of *Ps.* (*Nodiphillipsia*), reducing it exclusively to spatulate genal spines. *Ps.* (*Nodiphillipsia*) *spatulifera* was assigned to this subgenus and the species described in their article – *Ps.* (*Nodiphillipsia*?) aff. *obtusicauda*. Moreover, the species *obtusicauda* was assigned to *Ps.* (*Nodiphillipsia*?) is conditional, and in some places in this publication the type species *spatulifera* belongs [sic!] to the subgenus *Ps.* (*Pseudophillipsia*).

It is important to understand that neither the holotype of *Pseudophillipsia* (*Nodiphillipsia*) *obtusicauda*, nor on the type material of *Ps.* (*Nodiphillipsia*) aff. *obtusicauda* has no preserved genal spines, so it is difficult to compare their structure with that of *Ps.* (*Nodiphillipsia*) *spatulifera*.

The presence of *Ps.* (*Nodiphillipsia*) is apparently redundant, and its distinctive feature in the form of spatulate genal spines is at the species level, not the generic level, since the generic taxonomy of proetids is based solely on the morphology of the cranium and then the pygidium. All types of *Ps.* (*Nodiphillipsia*) should be classified as *Pseudophillipsia*, and the subgenus itself should be synonymized with the genus *Pseudophillipsia*, which is no longer divided into subgenera in this work (Figure 9).

Undoubtedly, it is necessary to conduct a detailed revision of all known species and species determined in open nomenclature of *Pseudophillip-*

sia, of which more than 46 are already known (Table 10). Some of them are described exclusively from pygidia and may well be representatives of *Ditomopyge* (*Carniphillipsia*).

Species. 42 species and five species determined in open nomenclature (Table 10).

Occurrence. Pennsylvanian (Moscovian) – Lopingian (Changhsingian); Eurasia and Africa (Tunisia).

Pseudophillipsia solida Weber, 1944
Figure 10A–D

- 1944 *Pseudophillipsia* (?) *solida* – Weber, p. 13–14, pl. II, fig. 8,9.
- 1957 *Delaria solida* – Goldring, p. 197.
- 1970 *Pseudophillipsia solida* – Hahn and Hahn, p. 304, 314–315.
- 1970 *Pseudophillipsia solida* – Hahn, Hahn, and Ramovš, p. 314–316, pl. 1, fig. 4, abb. 2.
- 1975 *Pseudophillipsia solida* – Hahn and Hahn, p. 17.
- 1983 *Pseudophillipsia solida* – Owens, p. 28.
- 1984a *Pseudophillipsia* (*Nodiphillipsia*) *solida* – Kobayashi and Hamada, p. 24,25,28.
- 1984a *Pseudophillipsia* (*Pseudophillipsia*) *solida* – Kobayashi and Hamada, p. 51.
- 1984a *Pseudophillipsia* (?) *solida* – Kobayashi and Hamada, p. 58.
- 2001 *Pseudophillipsia* (*Pseudophillipsia*) *solida* – Hahn, Hahn, and Brauckmann, S. 273,276.

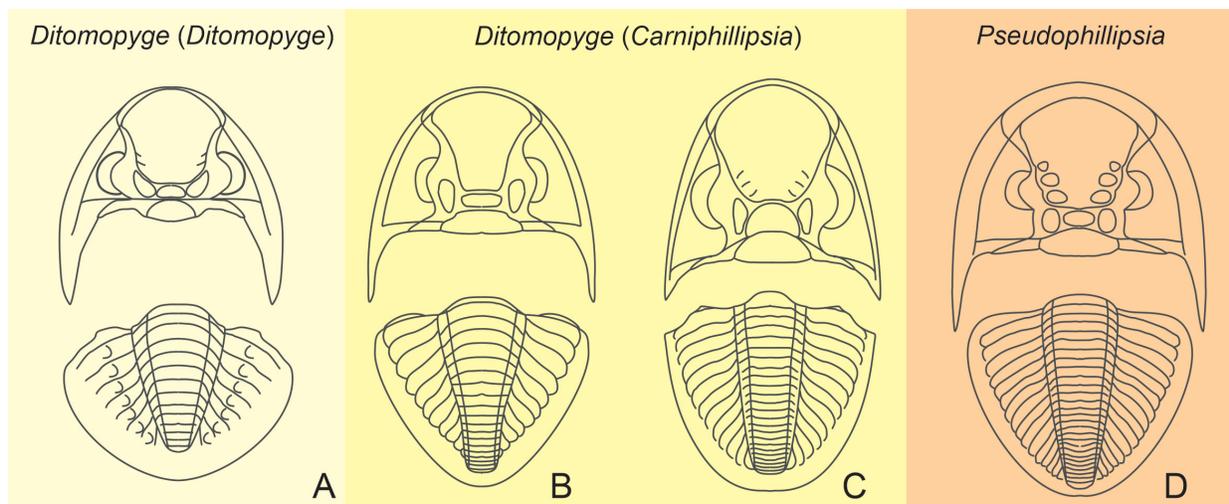


FIGURE 9. The difference between members of *Ditomopyge* (*Ditomopyge*), *Ditomopyge* (*Carniphillipsia*) and *Pseudophillipsia*; **A – D.** (*D.*) *scitula*, type species; **B – D.** (*C.*) *ovigalis*, type species; **C – D.** (*C.*) *paffenholzi*; **D – Ps.** *sumatrensis*, type species.

TABLE 10. Known species of *Pseudophillipsia* accepted in this work (those described exclusively by pygidia are conditionally classified as *Pseudophillipsia*).

Species	Part	Stratigraphy	Geography
<i>Ps. sumatrensis</i> (Roemer, 1880)	Cc, Hy	Guadalupian, Wordian	Indonesia, the western coast of Sumatra
<i>Ps. obtusicauda</i> (Kayser, 1883)	Cr, Py	Lopingian	Southern China
<i>Ps. (?) oehlerti</i> (Gemmellaro, 1892)	Py	Guadalupian, Roadian	Italy, Sicily, Sosio River Valley
<i>Ps. elegans</i> Gemmellaro, 1892	Cph, Th, Py	Guadalupian, Roadian	Italy, Sicily, Sosio River Valley
<i>Ps. (?) sosiensis</i> (Gemmellaro, 1892)	Py	Guadalupian, Roadian	Italy, Sicily, Sosio River Valley
<i>Ps. (?) acuminata</i> Mansuy, 1912	Py	Guadalupian, graywacke with <i>Lyttonia</i> cf. <i>tenuis</i>	Laos, Luang Prabang (Ban-Pak-Luang and Xieng Men)
<i>Ps. gemmellaro</i> i Canavari in Greco, 1935	Cc	Guadalupian, Roadian	Italy, Sicily, Sosio River Valley
<i>Ps. borissiaki</i> Tumanskaya, 1935	Cc	Guadalupian, Roadian	Crimea, Dzhen-Sofu (=Totai-Koi) Block on the Salgir River
<i>Ps. (?) crimensis</i> Tumanskaya, 1935	Py	Guadalupian, Roadian	Crimea, Kichkhi-Burnu Block on the Marta River
<i>Ps. (?) ibrischensis</i> Tumanskaya, 1935	Py	Guadalupian, Roadian	Crimea, Kichkhi-Burnu Block on the Marta River
<i>Ps. (?) martensis</i> Tumanskaya, 1935	Py	Guadalupian, Roadian	Crimea, Kichkhi-Burnu Block on the Marta River
<i>Ps. (?) mustafensis</i> Tumanskaya, 1935	Py	Guadalupian, Roadian	Crimea, Dzhen-Sofu (=Totai-Koi) Block on the Salgir River
<i>Ps. (?) sarabensis</i> Tumanskaya, 1935	Py	Guadalupian, Roadian	Crimea, Kichkhi-Burnu block on the Marta River
<i>Ps. (?) timorensis</i> (Gheyselinck, 1937)	Py	Guadalupian	Indonesia, East Nusa Tenggara Province, Basleo faunas
<i>Ps. solida</i> Weber, 1944	Cph, Cr	Lopingian, Changhsingian	Russia, Krasnodar Krai and Slovenia
<i>Ps. (?)</i> cf. <i>mustafensis</i> Tumanskaya, 1935 (in Weber, 1944)	Py	Lopingian, Changhsingian	Russia, Krasnodar Krai
<i>Ps. (?) caucasica</i> Weber, 1944	Py	Lopingian, Changhsingian	Russia, Krasnodar Krai
<i>Ps. (?) armenica</i> Weber, 1944	Py	Guadalupian	Armenia and Iran
<i>Ps. (?) hungarica</i> (Schréter, 1948)	Cr, Lg, Py	Lopingian, Nagyvisnyó Formation	Hungary, Bükk Mountains
<i>Ps. aff. sumatrensis</i> (Roemer, 1880) (in Hahn et al., 1970)	Cph, Py	Lopingian, Changhsingian, Bellerophon Formation	Slovenia, Vrzdenc
<i>Ps. (?)</i> cf. <i>hungarica</i> (Schréter, 1948) (in Hahn et al., 1970)	Py	Lopingian, Changhsingian, Bellerophon Formation	Slovenia, Žažar
<i>Ps. azzouzi</i> Termier et Termier 1974	Cc	Guadalupian, Capitanian	Tunisie, Djebel Tebaga
<i>Ps. anshunensis</i> Qian, 1977	Cph, Py	Lopingian, Wuchiapingian	China, Guizhou, Jiaozishan Section
<i>Ps. (?) subcircularis</i> Qian, 1977	Py	Lopingian, Wuchiapingian	China, Guizhou, Jiaozishan Section
<i>Ps. qinglongensis</i> Qian, 1977	Cph+Tx, Fr	Lopingian, Changhsingian, Dalong Formation	China, Guizhou, Zhongying Section
<i>Ps. (?) huishuiensis</i> Yin, 1978	Py	Cisuralian, Kungurian	China, Chengfanguan, Huishui County
<i>Ps. tongluensis</i> Ju in Zhang, 1982	Cc, Py	Guadalupian, Wordian–Capitanian, Dingjiashan Formation	China, Tonglu
<i>Ps. (?) wuweiensis</i> Zhang, 1982	Py	Guadalupian, Qixia Formation	China, Anhui, Wuwei County
<i>Ps. shanggaensis</i> Zhang, 1982	Cr	Lopingian, Wuchiapingian	China, Jiangxi, Shanggao County and Gao'an County, Loping Formation

TABLE 10 (continued).

Species	Part	Stratigraphy	Geography
<i>Ps. yunanxiensis</i> Liu, 1982	Cc	Cisuralian (?)	China, Sanzhi Count, Yunanxi
<i>Ps. akasakensis</i> Kobayashi et Hamada, 1984b	Cph+Py	Guadalupian, Roadian–Capitanian <i>Neoschwagerina</i> Zone (?) – <i>Yabeina</i> Zone	Japan, Gifu Prefecture, Akasaka Limestone
<i>Ps. ozawai</i> Kobayashi et Hamada, 1984b	Cr, Py	Guadalupian, Capitanian, <i>Yabeina</i> Zone	Japan, Gifu Prefecture, Akasaka Limestone
<i>Ps. aff. ozawai</i> Kobayashi et Hamada, 1984b (in Kobayashi and Sakagami, 1989)	Py	Lopingian, Changhsingian, Huai Thak Formation	Thailand, Lampang Province, Doi Pha Phlung
<i>Ps. kiriuensis</i> Kobayashi et Hamada, 1984b	Cr, Py	Guadalupian, Roadian–Capitanian, Nabeyama Formation <i>Parafusulina</i> Zone	Japan, Gunma and Gifu Prefecture
<i>Ps. (?) subtrigonalis</i> Kobayashi et Hamada, 1984a	Py	Guadalupian, Roadian–Capitanian, Nabeyama Formation	Japan, Tochigi Prefecture, Kuzuu
<i>Ps. (?) kuzuensis</i> Kobayashi et Hamada, 1984a	Py	Guadalupian Yamasuge limestone, Nabeyama Formation	Japan, Tochigi Prefecture, Kuzuu
<i>Ps. hanaokensis</i> Kobayashi et Hamada, 1984b	Cr, Py	Lopingian, Ichihashi Formation	Japan, Gifu Prefecture, Akasaka. Akasaka Limestone.
<i>Ps. (?) binodosa</i> Kobayashi et Hamada, 1984a	Py	Guadalupian, Wordian, Shigejizawa Formation	Japan, Anabuchi, Kesennuma City, Miyagi Prefecture, Myogo-sawa
<i>Ps. sasakii</i> Kobayashi et Hamada, 1984a	Cr, Py	Guadalupian, Wordian, Shigejizawa Formation	Japan, Anabuchi, Kesennuma City, Miyagi Prefecture, Myogo-sawa
<i>Ps. (?) simplex</i> Kobayashi et Hamada, 1984a	Py	Guadalupian, Wordian, Shigejizawa Formation	Japan, Anabuchi, Kesennuma City, Miyagi Prefecture, Myogo-sawa
<i>Ps. spatulifera</i> Kobayashi et Hamada, 1984a	Cc, Cr, Py	Guadalupian, Capitanian	Japan, Kanokura Formation (various localities)
<i>Ps. catena</i> Kobayashi et Hamada, 1984b	Cr, Py, Fr	Guadalupian, Roadian–Capitanian, <i>Neoschwagerina</i> Zone (?) – <i>Yabeina</i> Zone	Japan, Gifu Prefecture, Akasaka Limestone
<i>Ps. (?) perturbata</i> Hahn, Hahn et Ramovš 1990	Py	Guadalupian, Roadian	Crimea, Kichkhi-Burnu Block on the Marta River
<i>Ps. pradilla</i> Gandl, 2011	Cr, Py	Middle Pennsylvanian, Moscovian (Westphalian D)	Spain, Palencia, Blatt Cervera de Pisuerga,
<i>Ps. (?) aff. caucasica</i> Weber, 1944 (in Lerosey-Aubril, 2012)	Py	Lopingian, Nesen Formation	Iran, Alborz range, Yush
<i>Ps. (?) parvizii</i> Lerosey-Aubril, 2012	Py	Lopingian, Wuchiapingian, Dalan Formation	Iran, Dena Mountain, northwest of Yasouj
<i>Ps. darvazica</i> Mychko, 2016 nom. nud.	Cph	Cisuralian, Artinskian, Safetdaron Formation	Tajikistan, Darvaz, Obihingou River

2016 *Pseudophillipsia (Pseudophillipsia) solida* – Mychko, p. 263–264, pl. VI, fig. 6, 7.

2017 *Pseudophillipsia (?) solida* – Mychko and Alekseev, p. 68.

2020 *Pseudophillipsia (sensu lato) solida* – Schraut, 2020, p. 217, 218.

Lectotype. CNIGRMuseum, No. 79/5217, cephalon; Changhsingian, Lopingian; outcrop No. 127, 3,05 km from the estuary of the Urushten River, Malaya Laba River Basin, Krasnodar Krai, Russia;

Weber, 1944, pl. II, fig. 8a–c; designated by Hahn and Hahn (1970, p. 314).

Description. The cephalon is semi-elliptical, elongated. Genal spines apparently existed, but are unknown. The glabella is long, pear-shaped, strongly tapering towards the border margin. The border furrow is almost invisible, so the glabella in anterior passes into a narrow anterior border, steeply descending to the ventral side. In the posterior part of the glabella there are three pairs of



FIGURE 10. *Pseudophillipsia* from Lopingian of North Caucasus (A–J) and Guadalupian of Crimea (K); A–D – *Ps. solida* Weber, 1944: A, B – cephalon, CNIGRMuseum, No. 79/5217; C – incomplete cranidium, CNIGRMuseum, No. 80/5217; D – incomplete cranidium, CNIGRMuseum, No. 81/5217; E, F, G, H – *Ps. (?) caucasica* Weber, 1944: E – pygidium, CNIGRMuseum, No. 71/5217; F – pygidium, partial imprint, CNIGRMuseum, No. 72/5217; G – pygidium, CNIGRMuseum, No. 73/5217; H – deformed pygidium, CNIGRMuseum, No. 74/5217; I, J – *Ps. (?) cf. mustafensis* Tumanskaya, 1935: I – pygidium, CNIGRMuseum, No. 77/5217; J – fragment of pygidium, CNIGRMuseum, No. 78/5217; K – *Ps. (?) mustafensis* Tumanskaya, 1935, pygidium, CNIGRMuseum, No. 97/9733. Scale bars equal 5 mm.

small swollen lobes L_2 – L_4 . The medial preoccipital lobe is small, spherical and strongly convex; there are small teardrop-shaped lateral preoccipital lobes. The eyes are bean-shaped, large and high. The surface of the librigenae is convex, sharply defined by furrows from a broad border. The surface of the cephalon apparently contained no sculptural elements, with the exception of subtle terrace lines on the border.

Dimensions (Table 11).

Comparison. This species differs from other Lopingian representatives of *Pseudophillipsia* in the elongated glabella and almost complete reduction of the preglabellar furrow, causing the glabella to overhang the border furrow. However, in terms of the structure of the cranidium, the closest species (among the Lopingian) can be called *Ps. hanaokensis* Kobayashi et Hamada, 1984b.

Remarks. Apart from specimens of the type series *Pseudophillipsia solida* Weber, 1944, described from Changhsingian of the North Caucasus, the

TABLE 11. Dimensions (in mm) of cephalon, cranidia and glabellae of *Pseudophillipsia solida* Weber, 1944. LC – length of the cephalon, WC – width of the cephalon, LG – length of the glabella, LO – length of the occipital ring, WGA – width of the glabella at the anterior part, WGP – width of the glabella at the posterior part, LL – length of the L_1 lobes, LE – length of the eye.

Specimen	LC	WC	LG	LO	WGA	WGP	LL	LE
CNIGRMuseum, No. 79/5217	9	12	5.8	~1.5	5.5	2	1.3	2.4
CNIGRMuseum, No. 80/5217	-	-	9.5	>2	7.5	3.4	-	-
CNIGRMuseum, No. 81/5217	-	-	~5	-	4.5	-	-	-
GPIUL, No. 3853	-	-	7.4	>3	6	2.5	-	-
Average value	~9	~12	7.6	1.5	5.8	3	~1.3	2.4

TABLE 12. Known specimens of *Pseudophillipsia (?) solida* Weber, 1944; *localities at the North Caucasus (Malaya Laba River Basin).

Number of specimens	Part	Locality	Author of find, year	Photos
CNIGRMuseum, No. 79/5217	Cph	*3,05 km from the estuary of the Urushten River, outcrop No. 127	B.K. Likharev, 1927	Weber, 1944, pl. II, fig. 8; Mychko 2016, pl. VI, fig. 6; herein – Figure 10A, B
CNIGRMuseum, No. 80/5217	Cr	*3,05 km from the estuary of the Urushten River, outcrop No. 127	B.K. Likharev, 1927	Weber, 1944, pl. II, fig. 9; Mychko 2016, pl. VI, fig. 7; herein – Figure 10C
CNIGRMuseum, No. 81/5217	Cr	*Gefo Mount, outcrop No. 30 33 c.	B.K. Likharev, 1927	herein – Figure 10D
GPIUL, No. 3853	Cr	Slovenia, vicinity of the Vrzdenc Village	A. Ramovš, before 1970	Hahn, Hahn et Ramovš, 1970, pl. 1, fig. 4; herein – Figure 10D.

TABLE 13. Dimensions (in mm) of pygidia of *Pseudophillipsia (?) caucasica* Weber, 1944. LP – length of the pygidium, WP – width of the pygidium, WA – width of the axis at the anterior part, L/W – ratio of the length of the pygidium to its width, W/WA – ratio of the width of the pygidium to the width of the axis at the anterior part, DAB – distance from the end of the axis to edges of the border furrow of the pygidium. *the deformed (compressed from the sides) specimen.

Specimen	LP	WP	WA	L/W	W/WA	DAB
CNIGRMuseum, No. 71/5217	8.1	>8	~3.3	~1	~2.4	0.4
CNIGRMuseum, No. 72/5217	18.7	?	?	?	?	?
CNIGRMuseum, No. 73/5217	14.7	~14	4.8	~1	~2.9	1.3
CNIGRMuseum, No. 74/5217*	~9.2	~7	~2	<1.3	<3.5	~1
Average value	~12.7	~9.7	3.4	~1	~2.9	~0.9

cranidium depicted in the work of Hahn et al. (1970, taf. 1, fig. 4, abb. 2) was assigned to this species. They compared the the Slovenian cranidium and found similarities not so much with the lectotype (CNIGRMuseum, No. 79/5217), but with the paratype (CNIGRMuseum, No. 80/5217). The preservation of both cranidia does not allow us to attribute them to *Ps. solida*.

The pygidium is unknown for this species. It is quite possible that pygidia *Pseudophillipsia (?) caucasica* Weber, 1944 or *Ps. (?) mustafensis*

Tumanskaya, 1935, also known from the Changhsingian of the North Caucasus, may belong to this species. However, to test this hypothesis we need new finds, preferably complete exoskeletons, which we could confidently associate with *Ps. solida* Weber, 1944.

Occurrence. Changhsingian, Lopingian; Russia (Krasnodar Krai, North Caucasus) and Slovenia (vicinity of the village of Vrzdenc).

Material. Casts of the cephalon and two cranidia (Table 12).

Pseudophillipsia (?) *caucasica* Weber, 1944
Figure 10E–H

- 1944 *Pseudophillipsia elegans* Gemm. var.? *caucasica* – Weber, p. 5,6,12–13, pl. II, fig. 4.
1944 *Pseudophillipsia elegans* Gemm. var.? – Weber, p. 13, pl. II, fig. 2.
1957 *Pseudophillipsia elegans* Gemm. var.? *caucasica* – Goldring, p. 199.
1970 *Pseudophillipsia elegans caucasica* – Hahn and Hahn, p. 307.
1984a *Pseudophillipsia elegans caucasica* – Kobayashi and Hamada, p. 25,69.
2012 non *Pseudophillipsia* (s.l.) *armenica* – Lerosey-Aubril, 2012, p. 10, fig. 4 a.
2012 non? *Pseudophillipsia* (s.l.) *caucasica* – Lerosey-Aubril, 2012, p. 12.
2016 *Pseudophillipsia (Pseudophillipsia) caucasica* – Mychko, p. 62, 257–258, pl. VI, fig. 1, 2

Lectotype. CNIGRMuseum, No. 71/5217, pygidium; Changhsingian, Lopingian; blocks along the Tegen' River, Gefo Mount, Krasnodar Krai, Russia; Weber, 1944, pl. II, fig. 4; designated by Hahn and Hahn (1970, p. 307).

Description. Pygidium semi-elliptical, slightly elongated; axis long, trapezoidal in cross-section, high, reaches the pygidial border, but not reaching it; in anterior part of pygidium it quite wide, slightly tapering posteriorly; consists of 25+ rings separated by deep distinct furrows; lateral sides of axis constricted in central part, which is why each of rings has knee-shaped bend towards anterior part of pygidium; on dorsal side of each of rings pair of swellings which resemble flattened tubercles; dorsal furrows obvious; lateral lobes slightly convex,

relatively flattened; they consist of 11 pleural ribs, separated by deep interpleural furrows, widening towards pygidial border; in anterior part of pygidium, pleural ribs almost perpendicular to axis, but as they approach posterior edge they acquire longitudinal direction and sharp geniculate bend located on each rib closer to pygidial border; pleural furrows very narrow, barely noticeable; they observed on anterior ribs and located towards posterior side of each of ribs; no obvious sculpture on ribs; pygidial border wide and flattened; widest in posterior by part and decreasing towards anterior part of pygidium; terrace lines not noticeable.

Dimensions (Table 13).

Comparison. A very close species is *Pseudophillipsia hanaokensis* Kobayashi et Hamada, 1984b, as shown by the shape of the pygidium, and the number of axial rings and pleural ribs are equal in both species. The main difference between them is the wider pygidial border in *Ps. (?) caucasica*. From species determined in open nomenclature such as *Ps. (?) hungarica* (Schréter, 1948) and *Ps. (?) cf. hungarica* (Schréter, 1948), *Ps. (?) aff. caucasica* Weber, 1944 differs in a different number of segments, and most importantly, by the absence of single large tubercles on each of the pleural ribs. From *Ps. (?) subcircularis* Qian, 1977, which has a similar number of segments, differs by a narrower pygidium and a wider pygidial border.

Remarks. Lerosey-Aubril (2012, fig. 4a) shows the pygidium (holotype) of *Pseudophillipsia* (s.l.) *armenica*, described by Weber from the Wordian of Armenia, but the specimen label indicates that this specimen has the number CNIGRMuseum, No. 73/5217. This is undoubtedly an error: the specimen CNIGRMuseum, No. 73/5217 is a pygidium of *Pseudophillipsia* (?) *caucasica* (Table 14; Figure

TABLE 14. Known specimens of *Pseudophillipsia* (?) *caucasica* Weber, 1944; *incomplete specimen.

Number of specimens	Part	Locality	Author of find, year	Photos
CNIGRMuseum, No. 71/5217	Py*	Gefo Mount, blocks along the Tegen' River	V.N. Robinson, 1925	Weber, 1944, pl. II, fig. 4; Mychko 2016, pl. VI, fig. 2; herein – Figure 10 E
CNIGRMuseum, No. 72/5217	Py	2,25 from the estuary of the stream in Nikitinskaya Ravine	B.K. Likharev, 1927	herein – Figure 10 F
CNIGRMuseum, No. 73/5217	Py	Urushten tract (=paraje), outcrop No. 309	V.N. Robinson, 1925	Weber, 1944, pl. II, fig. 2; non (!) Lerosey-Aubril, 2012, p. 10, fig. 4 A; Mychko 2016, pl. VI, fig. 1; herein – Figure 10 G
CNIGRMuseum, No. 74/5217	Py	2,25 from the estuary of the stream in Nikitinskaya Ravine	B.K. Likharev, 1927	herein – Figure 10 H

10G), and the pygidium depicted by Lerosi-Aubril is actually numbered CNIGRMuseum, No. 75/5217.

In the same article (Lerosey-Aubril, 2012, p. 12) the *Pseudophillipsia* (s.l.) aff. *caucasica* from the Lopingian Nesen Formation of Iran is described. It is considered close to the North Caucasian species. He concludes the similarity between these species determined in open nomenclature partly from the fact that Weber (1944, p. 13 and table 2) mentions *Pseudophillipsia caucasica* in Armenia. However, Weber does not provide information about such a find anywhere else. The author of this article was also unable to find this specimen in the CNIGRMuseum collection No. 5217.

In *Pseudophillipsia* (s.l.) aff. *caucasica* from Iran, the smaller number of segments is striking (*Pseudophillipsia* (s.l.) aff. *caucasica* has more than 17 axial rings [apparently about 21–22] and about 10 pleural ribs, which is slightly less than in the North Caucasian species), as well as the presence in the Iranian species determined in open nomenclature large tubercles on the pleural ribs located at the geniculate bend, and then a number of small tubercles closer to the ends of the ribs. Also, the Iranian species does not have dorsal tubercles on the axial rings, similar to those of the North Caucasian. Similar morphological features are observed in the Slovenian *Pseudophillipsia* (?) cf. *hungarica*, but with some inconsistencies. For example, latter, like the North Caucasian one, has tubercles on the dorsal side of the axial rings, and single large tubercles on the pleural ribs are located closer to the dorsal furrows. Apparently, the Iranian species is either a new species, or is closely related of possibly an ontogenetic stage of another species, also found in Iran, but in another

Lopingian Dalan Formation – *Pseudophillipsia* (?) *armenica* Weber, 1944, since it has similar morphological features.

The North Caucasian species *Pseudophillipsia* (?) *caucasica* Weber, 1944 is represented exclusively by pygidia, so it can most likely belong to the genus *Pseudophillipsia* or the subgenus *Ditomopyge* (*Carniphillipsia*). It is likely that these pygidia may even belong to *Ps. solida* Weber, 1944, known from the same localities. Moreover, the pygidia and cephalae of *Ps. hanaokensis* are similar to those of *Ps. (?) caucasica* and *Ps. solida* respectively. Only the discovery of complete specimens of *Ps. (?) caucasica* and *Ps. solida* can resolve to this issue.

Occurrence. Changhsingian, Lopingian; Russia (Krasnodar Krai, North Caucasus).

Material. Four pygidia (Table 14).

Pseudophillipsia (?) cf. *mustafensis* Tumanskaya, 1935

Figure 10I–K

1944 *Pseudophillipsia mustafensis?* – Weber, 1944, p. 13, pl. II, fig. 3.

1970 [part.] *Pseudophillipsia mustafensis* – Hahn and Hahn, S. 309.

2016 [part.] *Pseudophillipsia (Pseudophillipsia) mustafensis* – Mychko, p. 260.

Description. Large pygidium, elliptical in shape, elongated; axis convex, long, reaching pygidial border and abutting against it; consists of 25 rings separated by narrow and deep furrows; axial rings geniculate on lateral sides of axis; on dorsal side of each of rings pair of small tubercles; lateral lobes of pygidium convex and bear 12 pleural ribs, separated by deep interpleural furrows; angle between pleural ribs and dorsal furrows hardly changes

TABLE 15. Dimensions (in mm) of pygidium of *Pseudophillipsia* (?) cf. *mustafensis* Tumanskaya, 1935. LP – length of the pygidium, WP – width of the pygidium, WA – width of the axis at the anterior end, L/W – ratio of the length of the pygidium to its width, W/WA – ratio of the width of the pygidium to the width of the axis at the anterior end, DAB – distance from the end of the axis to edges of the border furrow of the pygidium.

Specimen	LP	WP	WA	L/W	W/WA	DAB
CNIGRMuseum, No. 77/5217	7.5	~8,6	2,7	~0,9	~3	0,4

TABLE 16. Known specimens of *Pseudophillipsia* (?) cf. *mustafensis* Tumanskaya, 1935; *incomplete specimen, fragment of a lateral lobe.

Number of specimens	Part	Locality	Author of find, year	Photos
CNIGRMuseum, No. 77/5217	Py	Gefo Mount, outcrop No. 30	B.K. Likharev, 1927	Weber, 1944, pl. II, fig. 3; herein – Figure 10 I
CNIGRMuseum*, No. 78/5217	Py	Gefo Mount, outcrop No. 30	B.K. Likharev, 1927	herein – Figure 10 J

from anterior to posterior and ~30 degrees; each pleural rib ornamented with one row of medium-sized flattened tubercles; pygidial border wide and flattened; greatest width of pygidial border observed on lateral parts of pygidium, but decreases in posterior part.

Dimensions (Table 15).

Comparison. This pygidium is similar to *Ps. (?) mustafensis* Tumanskaya, 1935 (Figure 10K) from the Roadian of Crimea, however, the North Caucasian species determined in open nomenclature has a number of small tubercles on the pleural ribs, which are absent at the Crimean species. Also, the pygidial border of *Ps. (?) cf. mustafensis* is much wider than that of *Ps. (?) mustafensis*. *Ps. (?) caucasica* from coeval deposits of the North Caucasus differs primarily by the location of the pleural ribs in relation to the dorsal furrows: *Ps. (?) caucasica* has the posterior ribs that are almost parallel to the furrows, whilst in *Ps. (?) cf. mustafensis* their angle is close to perpendicular.

Occurrence. Changhsingian, Lopingian; Russia (Krasnodar Krai, North Caucasus).

Material. Two pygidia (Table 16).

LOPINGIAN TRILOBITE LOCALITIES

Currently, the Lopingian is divided into two stages, the Wuchiapingian and the Changhsingian, within the framework of the International Stratigraphic Scale (Figure 1). The stratotypes for both stages are located in China. The Wuchiapingian stratotype is located in the Penglaitan Section of Guanxi Province and the Changhsingian stratotype is located in the Meishan Section of Zhejiang Province. These two stratotypes were ratified in 2004 and 2005, respectively. In 2023, the lower boundary of the Wuchiapingian was revised and reaffirmed in the same region due to flooding at the original site at the Penglaitan Section.

The boundary between the Guadalupian (Capitanian) and Lopingian (Wuchiapingian) is defined by the appearance of the conodont *Clarkina postbitteri postbitteri*, which correlates with the major extinction of several Guadalupian groups of invertebrates, such as corals, fusulinids, ammonoids, brachiopods (Jin et al., 2006) and trilobites. The boundary between the Lopingian and the Lower Triassic is marked by the even more extensive extinction of groups – the Great Late Permian Extinction Event or EPME. This extinction event was also accompanied by various geochemical anomalies, magmatism of varying composition (Shen et al., 2019; and others), increasing ocean

temperatures (Chen et al., 2020) and others phenomena.

The radioisotopic age of the lower boundary of the Lopingian, or and of the Wuchiapingian, is currently 259.51 ± 0.21 Ma. The base of the Changhsingian is 254.14 ± 0.07 Ma. And the Changhsingian–Triassic boundary is 251.90 ± 0.03 Ma (Permophiles, 2023, p. 49). Therefore, the duration of the Lopingian Epoch was approximately 7.6 Ma.

Lopingian deposits are widely distributed, occurring on all continents, and are represented by both marine and terrestrial strata. For the purposes of this article, we will be focusing on marine Lopingian deposits, in which trilobites are known. In total, there are approximately 34 known localities of this type (Table 17) located in 11 different countries (Figure 11).

Slovenia. The most western Lopingian trilobites known were found to the east of Ljubljana in the area of the villages of Vrzdenc and Žažar (Hahn et al., 1970). These areas have Lopingian outcrops, from which Ramovš (1958a; 1958b) collected a rich marine fauna, associated with dark gray limestones. These deposits comprise as the Žažar Formation. Recent research suggests that this formation is identical to the Bellerophon Formation, which is widespread in the Carnic and Dolomite Alps in Austria and Italy (Kolar-Jurkovšek et al., 2018). According to their data, the presence of conodonts *Hindeodus praeparvus* conodonts in these formations allows us to correlate them with the uppermost part of the Changhsingian.

From outcrops of the Bellerophon Formation near the Vrzdencs Village there are two specimens of trilobites, represented by an incomplete cephalon with a pygidium of *Pseudophillipsia* n. sp. aff. *sumatrensis* (Roemer, 1880) and *Pseudophillipsia solida* Weber, 1944; near the Žažar Village – the pygidium of *Pseudophillipsia* (?) cf. *hungarica* (Schréter, 1948) (Hahn et al., 1970).

Unfortunately, no new trilobite finds have been reported from these localities in more than 50 years (Schraut, 2020, p. 217).

Hungary. Trilobites of *Pseudophillipsia* (?) *hungarica* (Schréter, 1948) from the Bükk Mountain in northeastern Hungary (Schréter, 1948) are found in black limestone, together with the brachiopods "*Lyttonia nobilis*" (Schréter, 1948). Currently this brachiopod species belongs to the genus *Leptodus*. For a long time, these finds were considered Guadalupian (e.g., Hahn and Hahn, 1970, p. 308; Kobayashi and Hamada, 1984a, p. 23), until Detre (1991) reported their Lopingian age, and also that

TABLE 17. Distribution of Lopingian trilobites in the World. Lop – undivided Lopingian deposits, Wu – Wuchiapingian, Ch – Changhsingian.

Locality	Formation	Stage	Species / forms	References
Vrzdeneč (Slovenia)	Bellerophon Fm. (formed Žažar Fm.)	Ch.	<i>Pseudophillipsia</i> n. sp., aff. <i>sumatrensis</i> (Roemer, 1880) <i>Pseudophillipsia solida</i> Weber, 1944	Hahn et al., 1970; Hahn, Hahn et Brauckman, 2001
Žažar (Slovenia)	Bellerophon Fm. (former Žažar Fm.)	Ch.	<i>Pseudophillipsia</i> (?) cf. <i>hungarica</i> (Schréter, 1948)	Hahn et al., 1970; Hahn, Hahn, Brauckman, 2001
Bükk Mountains (Hungary)	Nagyvisnyó Fm.	Ch.	<i>Pseudophillipsia</i> (?) <i>hungarica</i> (Schréter, 1948)	Schréter, 1948; Detre, 1991
Crimea, blocks on the river Alma	-	Lop.?	<i>Pseudophillipsia</i> (?) sp. ind. № 1 <i>Pseudophillipsia</i> (?) sp. ind. № 2 <i>Pseudophillipsia</i> sp. ind. № 1	Tumanskaya, 1935
Far East, Nakhodka	Lyudyanzian	Wu.	<i>Paraphillipsia</i> sp. <i>Neogriffithides</i> (?) sp.	Herein
North Caucasus	Nikitino and Urushten Fm's.	Ch.	<i>Brachymetopus (Acutimetopus) caucasicus</i> Licharew in Weber, 1944 <i>Kathwaia caucasica</i> (Weber, 1944) <i>Paraphillipsia urushtensis</i> sp. nov. <i>Pseudophillipsia</i> (?) <i>caucasica</i> Weber, 1944 <i>Pseudophillipsia mustafensis</i> Tumanskaya, 1935 <i>Pseudophillipsia solida</i> Weber, 1944	Weber, 1944; this research
Alborz range, Yush (Iran)	Nesen Fm.	Wu.–Ch.	<i>Acropyge weggeni</i> Hahn et Hahn, 1981 <i>Pseudophillipsia</i> aff. <i>caucasica</i> Weber, 1944	Hahn and Hahn, 1981; Hahn, Hahn et Brauckman, 2001; Lerosey-Aubril, 2012
Dena Mountain, northwest of Yasouj (Iran)	Dalan Fm.	Wu.	<i>Pseudophillipsia</i> (?) <i>parvizii</i> Lerosey-Aubril, 2012	Lerosey-Aubril, 2012
Salt Range, Zaluch Nala–Kala Wahan (Pakistan)	Wargal Fm.	Wu.	<i>Ditomopyge (Carniphillipsia) fatmii</i> Grant, 1966	Grant, 1966; Hahn, Hahn et Brauckman, 2001
Salt Range, Kathwai–Kushab (Pakistan)	Wargal Fm.	Wu.	<i>Kathwaia caucasica</i> (Weber, 1944) (= <i>Kathwaia capitorosa</i> Grant, 1966)	Grant, 1966; Hahn, Hahn et Brauckman, 2001; this research
Tibet, Zanda County (China)	Chitichun Limestone	Wu. (?)	<i>Cheiropyge himalayensis</i> Diener, 1897 <i>Paraphillipsia</i> (?) <i>middlemissi</i> Diener, 1897	Diener, 1897; Hahn, Hahn et Brauckman, 2001
Tibet, Shuanghu (China)	Raggyorcak a Fm.	Ch. (?)	<i>Ditomopyge (Carniphillipsia) raggyorcakaensis</i> (Qian 1981)	Qian, 1981; Hahn, Hahn et Brauckman, 2001
Chongqing, Beifengjing Section (China)	Changxing Fm.	Ch.	<i>Pseudophillipsia obtusicauda</i> (Kayser, 1883) <i>Ditomopyge (Carniphillipsia) chongqingensis</i> (Lu, 1974) <i>Pseudophillipsia</i> sp.	Shen and He, 1991
Chongqing, Tudiya buildup (China)	Changxing Fm.	Ch.	<i>Ditomopyge (Carniphillipsia) cf. chongqingensis</i> (Lu, 1974)	Reinhardt, 1988
Chongqing, Daijiagou Beipei, Yanjingxi section (China)	Changxing Fm.	Ch.	<i>Pseudophillipsia</i> (?) sp.	Shen et al., 1995; Yang et al., 1987
Chongqing, Liziya section (China)	Longtan Fm.	Wu.	<i>Pseudophillipsia</i> (?) sp.	Zeng et al., 1995
Chongqing, Huaying Section (China)	Changxing Fm.	Ch.	<i>Pseudophillipsia obtusicauda</i> (Kayser, 1883) <i>Ditomopyge (Carniphillipsia) chongqingensis</i> (Lu, 1974)	Yang et al., 1987
Chongqing, Wenxing (China)	Longtan Formation	Wu.	<i>Ditomopyge (Carniphillipsia) lui</i> (Kobayashi et Hamada, 1984a) <i>Ditomopyge (Carniphillipsia) chongqingensis</i> (Lu, 1974)	Lu, 1974; Kobayashi and Hamada, 1984a

TABLE 17 (continued).

Locality	Formation	Stage	Species / forms	References
Chongqing, Zhongliangshan (China)	Changxing Fm.	Ch.	<i>Ditomopyge (Carniphillipsia) cf. chongqingensis</i> (Lu, 1974)	Shi et al., 2016
Guizhou, Jiaozishan Section (China)	Longtan Fm.	Wu.	<i>Pseudophillipsia anshunensis</i> Qian, 1977 <i>Pseudophillipsia (?) subcircularis</i> Qian, 1977	Qian, 1977; Kobayashi and Hamada, 1984a
Guizhou, Yanbeihou (China)	Longtan Fm.	Wu.	<i>Pseudophillipsia (?)</i> sp.	Wang et al., 2011
Guizhou, Xinmin section (China)	Dalong Fm.	Ch.	<i>Ditomopyge (Carniphillipsia) cf. chongqingensis</i> (Lu, 1974)	Feng et al., 2011
Guizhou, Tianshengqiao (China)	Dalong Fm.	Ch.	<i>Acropyge brevica</i> Yin, 1978	Yin, 1978
Guizhou, Wenjiangsi Section (China)	Changxing Fm.	Ch.	<i>Pseudophillipsia obtusicauda</i> (Kayser, 1883) <i>Ditomopyge (Carniphillipsia) chongqingensis</i> (Lu, 1974)	Shen and He, 1994
Guizhou, Zhongying Section (China)	Dalong Fm.	Ch.	<i>Pseudophillipsia qinglongensis</i> Qian, 1977 <i>Ditomopyge (Carniphillipsia) pyriformis</i> (Qian, 1977) <i>Acropyge multisegmenta</i> Qian, 1977	Qian, 1977
Guangxi, Heshan Section and Paoshui Section (China)	Heshan Fm.	Wu.	<i>Ditomopyge (Carniphillipsia) heshanensis</i> (Qian, 1977) <i>Pseudophillipsia obtusicauda</i> (Kayser, 1883)	Qian, 1977; Yang et al., 1987
Guangdong, Qujiang County (China)	Changxing Fm.	Ch.	<i>Ditomopyge (Carniphillipsia) lui</i> (Kobayashi et Hamada, 1984a)	Zhou, 1977; Kobayashi and Hamada, 1984a
Jiangxi, Shanggao County and Gao'an County (China)	Loping Formation, Laoshan Member	Wu.	<i>Pseudophillipsia shanggaoensis</i> Zhang, 1982 <i>Cheiropyge (?) gaoanensis</i> Zhang, 1982	Zhang, 1982
Jiangxi, Shanggao County and Leping County (China)	?	Lop.	<i>Pseudophillipsia obtusicauda</i> Kayser, 1883	Kayser, 1883; Zhang, 1982
West Timor, Kali-Mati (Indonesia)	Amarassi Beds	Wu.	<i>Timorcranium parvulum</i> (Beyrich, 1865)	Beyrich, 1865; Hahn et Brauckmann, 1975; Brauckmann and Gröning, 2013
Gifu Prefecture, Akasaka (Japan)	Akasaka Limestone, Ichihashi Fm.	Lop.	<i>Pseudophillipsia hanaokensis</i> Kobayashi et Hamada, 1984b	Kobayashi and Hamada, 1984a; 1984b
Lampang Province, Doi Pha Phlung and Huai Mae Phlung (Thailand)	Huai Thak Fm.	Ch.	<i>Pseudophillipsia aff. ozawai</i> Kobayashi et Hamada, 1984a	Kobayashi and Sakagami, 1989; Ishibashi, 1998
Mossburn, Oreti River (New Zealand)	Countess Fm., Stephens Subgroup	Ch. (?)	<i>Triporetus</i> sp.	Hyden et al., 1982
Spitsbergen, Ahlstrandhalvøya peninsula	Kapp Starostin Fm., Hovtinden member	Lop.	<i>Triporetus borealis</i> Kobayashi, 1987	Kobayashi, 1987

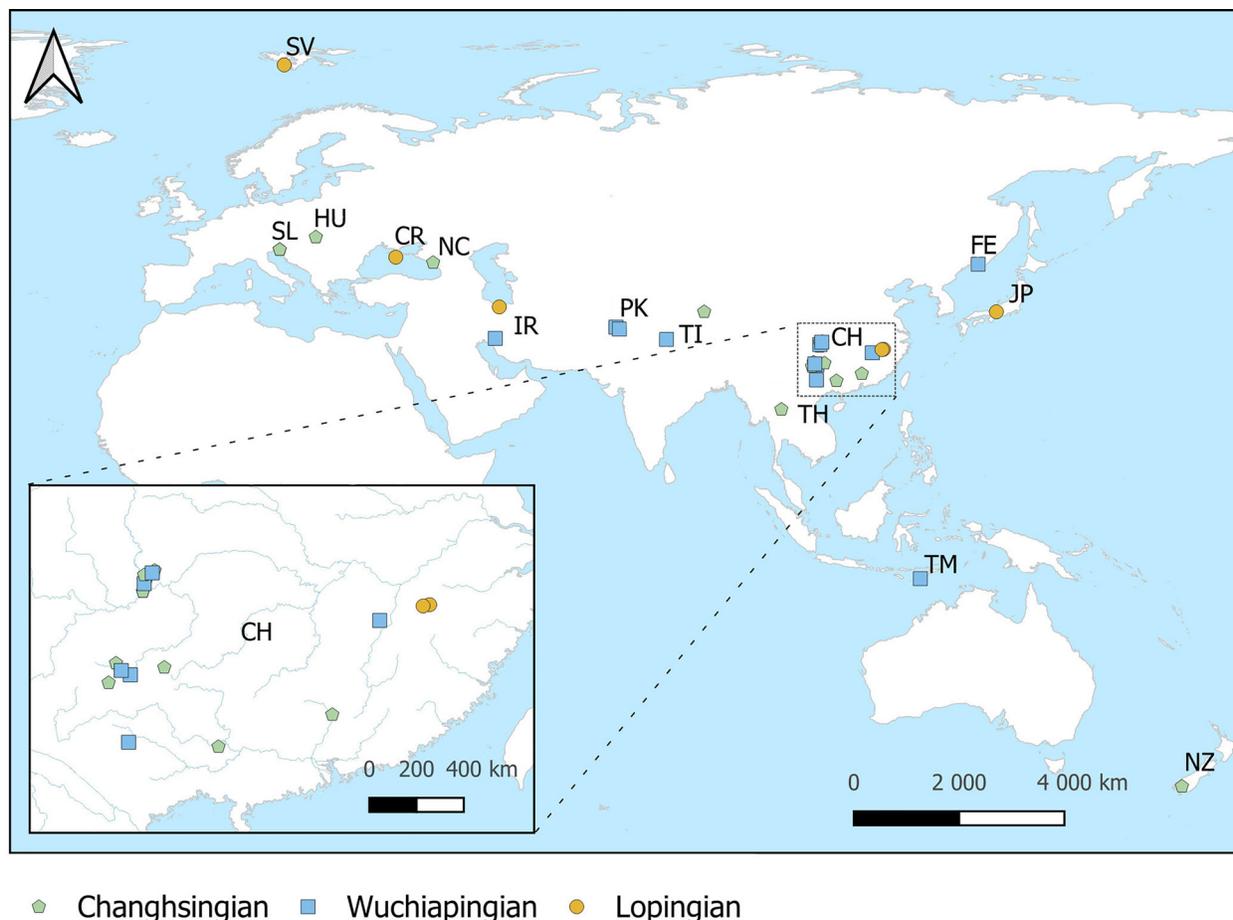


FIGURE 11. Lopingian trilobite localities: SV – Spitsbergen, SL – Slovenia, HU – Hungary, CR – Crimea, NC – North Caucasus, FE – Far East, IR – Iran, PK – Pakistan, TI – Tibet, CH – Southern China, TH – Thailand, JP – Japan, TM – Timor, NZ – New Zealand.

that over 40 years a fairly extensive collection of trilobites (more than 100 specimens) from the deposits under discussion has accumulated. In this publication, Detre argues that the Lopingian trilobites from the Bükk Mountains represent the latest in Europe. He did not take into consideration, however, the publication by Hahn, Hahn and Ramovš (1970) describing trilobite remains from Slovenia. I note that Owens in his work (2003) indicates the Lopingian age for trilobites found in Hungary.

Indeed, Lopingian deposits are widespread in the Bükk Mountains. The Nagyvisnyó Formation, which consists of black limestone is most likely of Changhsingian (Posenato et al., 2005; Brookfield et al., 2021). The fact that trilobites occur in the upper part of the formation has also been indicated in more recent works (Brookfield et al., 2021, p. 80).

Crimea. Trilobites have been found in Late Palaeozoic blocks of Permian shallow-water organogenic

limestones, up to 20–100 m in diameter. These are exposed on the northwestern side of the Crimean Mountains. The sandy-clay strata of the Eskiorda Formation (or Group), which dates back to the Upper Triassic–Lower Bajocian, are characterized by relatively shallow water facies of the Tauride Flysch Group.

Palaeozoic “rootless” limestone blocks were discovered in Crimea by Fokht (1901) and have been described in numerous publications. According to many researchers (e.g., Miklouho-Maclay and Muratov, 1958, p. 34), these blocks are parts of massifs that slid from uplifts into the immersion zone. Smaller boulders and pebbles are a result of their erosion.

The limestone of these blocks contains remains of a diverse marine invertebrate fauna, including fusulinids, ammonoids, trilobites and brachiopods; less common are bivalves and gastro-

Pods, solitary rugose corals and bryozoans (Grunt and Novikova, 2002).

Trilobites from these blocks have been known for quite a long time: these arthropods were discovered by Weber (1915), and later a number of species and species determined in open nomenclature were described by Tumanskaya (1930, 1935). There are also more recent finds (Mychko, 2012).

In total, there are three main localities in Crimea where trilobite have been found: the Kichkhi-Burnu blocks on the Marta River, the Dzhen-Sofu (=Totai-Koi) block on the Salgir River and blocks along the Alma River. Based on recent stratigraphic research (Pronina and Nestell, 1997; Kotlyar et al., 1999b), the first two block complexes, while most likely of Guadalupian, the blocks on the Alma River contain geologically younger limestones. They contain assemblages of small foraminifera and fusulinids characteristic of the upper Median–Dorashamian stage of the Tethyan scale. This roughly corresponds to the upper Capitanian–Changhsingian stages of the ICS (Leven, 2009).

However, the exact position and age of these blocks, from which trilobites were described by Tumanskaya, is now very difficult to determine due to changes in the landscape (since the time of her research, the area has been heavily forested, in 1966 the Partizansk Reservoir was constructed, and the exact locality is not known). Therefore, I consider the trilobite specimens described by Tumanskaya as very likely to be of the Lopingian.

In the boulders of the Alma River, Tumanskaya (1935, p. 10) found difficult-to-identify pygidia, which she conditionally assigned to the genus *Pseudophillipsia*.

North Caucasus. The stratigraphy of Lopingian (Changhsingian) trilobite localities in the North Caucasus is described in this article. The trilobite fauna of this area is relatively diverse and includes the following species: *Brachymetopus (Acutimetopus) caucasicus* Licharew in Weber, 1944, *Paraphillipsia urushtensis* sp. nov., *Kathwaia caucasica* (Weber, 1944), *Pseudophillipsia solida* Weber, 1944, *Pseudophillipsia (?) caucasica* Weber, 1944 and *Pseudophillipsia (?) mustafensis* Tumanskaya, 1935.

Far East. During a recent fieldwork (July 2024) by the author in the Russian Far East (Primorsky Krai), trilobites were discovered in Upper Permian here. The Nakhodka Reef locality is located in the Nakhodka city. It is one of the large carbonate bodies among the organogenic structures of the

Guadelupian-Lopingian of Far East and has a complex structure. Trilobites were found in sandy limestones of the upper part, confined to the Lyudyanzian Substage (Lower Wuchiapingian). I have previously assigned these trilobites to genera *Paraphillipsia* and *Neogriffithides* (?). Herein, I only briefly report on them.

Iran. In this area, at least two localities for Lopingian trilobites are known, one of which is located in the north in the Alborz Mountains of Mazandaran province, near the village of Yush. Here Hahn and Hahn (1981) described three forms: *Acropyge weggeni* Hahn and Hahn, 1981, *Acropyge?* sp. indet. and *Iranaspidion* sp. indet, which are represented by pygidia. In a subsequent revision of these specimens, Lerosey-Aubril (2012) assigned the *Acropyge?* sp. indet. to the species *Acropyge weggeni* Hahn and Hahn, 1981, and identified the pygidium of *Iranaspidion* sp. indet as *Pseudophillipsia* (s.l.) aff *caucasica* Weber, 1944, closely related to the Northern Caucasian species.

The specimens are from the Nesen Formation, which is represented in the locality by wackestones with bivalves, brachiopods, bryozoans, crinoids, gastropods, ostracods and, in fact, trilobites (Lerosey-Aubril, 2012, p. 4). According to Lerosey-Aubril's research, the foraminiferal assemblage belongs to the Wuchiapingian. However, later studies (Forel et al., 2015) indicate that the Nesen Formation is approximately 130 m thick and consists of marly and siliceous limestones. It is divided into lower and upper members. The first 10-15 m of the formation may belong to the upper part of the Upper Capitanian (Angiolini et al., 2010), while the rest of the lower part is characterized by the presence of *Araxilevis intermedius* Biozone, indicating an Early Wuchiapingian age for the formation. The presence of the conodont *Hindeodus julfensis* (Sweet) in this formation suggests a Late Wuchiapingian – Early Changhsingian age (Forel et al., 2015). However, it is not entirely clear which part of the formation the trilobite originates from.

From another locality in southern Iran, located on the Dena Ridge (Zagros Mountains, approximately 58 km northwest of Yasuj, Kohgiluyeh and Boyer-Ahmad provinces), different species of *Pseudophillipsia (?) parvzii* Lerosey-Aubril, 2012 has been identified, described by well-preserved pygidia. The discovery was made in dark gray sandy wackestone along with gastropods, brachiopods, bryozoans, crinoids, ostracods and foraminifera (Lerosey-Aubril, 2012, p. 12). This

wackestone belongs to the Dalan Formation, and the Wuchiapingian age of the deposits can be determined by the presence of the fusulinids, such as *Codonofusiella* ex gr. *tenuissima* (Lerosey-Aubril, 2012, p. 4).

Pakistan. In the Permian deposits, exposed on the Salt Range, two localities are known from which trilobites originate. They were discovered by Grant and Fatmi in 1963–64 and were later described by Grant (1966).

In the first locality, located between the villages of Zaluch Nala and Kala Wahan in the “Middle *Productus* limestone”, two enrolled exoskeletons of *Ditomopyge fatmii* Grant, 1966 were found. This species is classified as belonging to the subgenus *Ditomopyge (Carniphillipsia)* Hahn and Brauckmann, 1975 in this article.

According to recent research, the “Middle *Productus* limestone” is correlated with the upper part of the Wargal Formation (Sameeni, 2009, p. 69) and is estimated to be of Wuchiapingian age (Mertmann, 2003; Jin et al., 2006).

Another locality is located on the road between Kathwai and Kushab, approximately 9 km south of Kathwai. From here Grant (1966) described *Kathwaia capitorosa* by its well-preserved enrolled exoskeleton. In this work, it was considered to be a synonym for *Kathwaia caucasica* (Weber, 1944). This find also came from the Wargal Formation.

China. The largest number of localities and the number of Lopingian trilobites has been discovered in China. This is mainly due to the widespread distribution of the Lopingian sections here, their completeness, accessibility and their better study compared to other sections around the world.

Tibet. In the Himalayas, in Zanda County, Ngari Prefecture, pygidia were discovered and described by Diener (1897) as two new species: *Cheiropyge himalayensis* Diener, 1897 and *Phillipsia middlemissi* Diener, 1897. These findings come from isolated blocks Chitichun Limestone (Block No. 1).

The age of these limestone blocks is controversial. At the time of C. Diener, these formations were considered to be Permian-Carboniferous, but their ages have since been revised. Thus, Hahn, Hahn and Brauckman (2001) noted that the presence of ammonoids of the genus *Cyclolobus* here indicates the Wuchiapingian age of the Chitichun Limestone. However, representatives of this genus of ammonoids are also found in the Guadalupian (Leonova, 2010).

In modern stratigraphic studies (Shen and Shi, 2004), the Chitichun Limestone is considered

to be a tentative Capitanian formation. However, the authors note that the collections of ammonoids, brachiopods and foraminifera from this formation include Wuchiapingian genera and species, and their stratigraphic reference requires clarification. In this work, I conditionally assign the Chitichun Limestone to the Wuchiapingian.

It is interesting that in the work of Hahn, Hahn and Brauckman (2001), only *Cheiropyge himalayensis* is indicated for the Lopingian of Tibet, and the second species *Phillipsia middlemissi* is not mentioned despite the fact that they both originate from the same locality. Moreover, in Hahn and Hahn (2008), *Phillipsia middlemissi* conditionally assigned the subgenus *Cummingella?* (*Cummingella?*), and the stratigraphic interval for it is indicated as the Cisuralian or Permian-Carboniferous. It is worth noting that *Phillipsia middlemissi* has been classified in various genera for a long time: *Ditomopyge*, *Neoproetus* and *Paraphillipsia*. However, Owens (2003, p. 380) indicates the Wuchiapingian of the Himalayas for the genus *Paraphillipsia*, which obviously means the definition of the species under discussion as *Paraphillipsia middlemissi*. I also classify this species tentatively as *Paraphillipsia*.

Much further north, but also from Tibet, the cranidium and pygidium of *Ditomopyge (Carniphillipsia) raggyorcakaensis* (Qian, 1981) are described from the Raggyorcaka Formation in Shuanghu County (Qian, 1981). The Raggyorcaka Formation has Lopingian, presumably Changhsingian age (Qiao et al., 2021).

Chongqing Municipality. There are several Lopingian trilobite localities in the vicinity of Chongqing. In the Beifengjing Section, in the Changxing Formation, layers 9–28, consisting of limestones, mudstones and wackestones, there are trilobites *D. (C.) obtusicauda* (Kayser, 1883), *Ditomopyge (Carniphillipsia) chongqingensis* (Lu, 1974) and *Pseudophillipsia* sp. These remains are found in association with a very diverse fauna of bivalves, brachiopods and cephalopods (Shen and He, 1991). Unfortunately, this work does not contain images of trilobites, and they are only in the list of faunas.

From the Longtan Formation of the Wuchiapingian age near Wenxing Town come finds of *D. (C.) lui* (Kobayashi et Hamada, 1984a) and *Ditomopyge (Carniphillipsia) chongqingensis* (Lu, 1974), which were found together with various corals and brachiopods (Lu, 1974; Wu and Wang, 1974; Shen and Shi, 2004).

Further north, in the lower part of the Changxing Formation of Changhsingian age, one isolated pygidium, identified as *Pseudophillipsia* cf. *chongqingensis*, was discovered near the so-called Tudiya buildup (Reinhardt, 1988, p. 258).

In the same formation, but even further north in another section of Daijiagou Beipei, trilobites have been found *Pseudophillipsia* sp. in limestone with brachiopods, bryozoans and conodonts *Xaniognathus elongatus*, *Hindeodus minutus* and *Clarkina changxingensis* (Shen et al., 1995, p. 21).

North of Daijiagou, in the Yanjingxi Section in the Changxing Formation, there are references to the presence of *Pseudophillipsia* sp. (Yang et al., 1987). Specimens of *Pseudophillipsia* sp. noted here and in oldest, Wuchiapingian deposits of the Longtan Formation of the Liziya Section (Zeng et al., 1995). *Pseudophillipsia obtusicauda* (Kayser, 1883) and *Ditomopyge (Carniphillipsia) chongqingensis* (Lu, 1974) are known from the Changxing Formation of the Huaying Section located in Linsui County (Yang et al., 1987).

One of the interesting localities of Lopingian trilobites is known in Chongqing in the volcanic ash beds of the Zhongliangshan Section (Shi et al., 2016). There complete exoskeletons and numerous remains considered *Ditomopyge (Carniphillipsia)* cf. *chongqingensis* (Lu, 1974) have been found.

Guizhou Province. From the Jiaozishan Section in the Anshun urban district, Qian (1977) described two new species *Pseudophillipsia anshunensis* Qian, 1977 and *Pseudophillipsia subcircularis* Qian, 1977. According to his data, they originate from deposits (layer 16) together with *Nankinella* sp., *Sphaerulina* sp. and *Lepingoceras* (?) sp., which indicate their Lopingian, most likely Wuchiapingian age. The Lopingian age of these deposits is confirmed by other researchers (Wang et al., 2011).

From the nearby Xinmin Section come trilobite pygidia and cephalons identified as *Pseudophillipsia* sp. (Feng et al., 2011, fig. 3). They were found in carbonaceous mudstone interbeds of bentonites overlain by marl with the conodont *Clarkina meishanensis* and, apparently, are the youngest trilobites known to science. In this article they are considered as *Ditomopyge (Carniphillipsia)* cf. *chongqingensis* (Lu, 1974).

From the Longtan Formation of the Wuchiapingian age in the Yanbeihou K12 section in Zhijin County, the remains of *Pseudophillipsia* sp. are mentioned (Wang et al., 2011, p. 171).

From the Dalong Formation of the Tianshengqiao Section of Nayong County, a new species *Acropyge brevica* Yin, 1978 was described from the cranidium and pygidium. The Dalong Formation is Changhsingian formation (Liu et al. 2019).

At the Guiyang Mineral Exploration Factory in Guiyang City, a variety of trilobites were collected in the Wuchiapingian of the Maokou Formation, described as new species (Yuan et al., 1992): *Acanthophillipsia* (?) *granulosa* Yuan et al., 1992, *Acanthophillipsia guiyangensis* Yuan et al., 1992, *Acanthophillipsia abnormis* Yuan et al., 1992 and *Acanthophillipsia abrota* Yuan et al., 1992. According to the paleobioDB.org database, these deposits contain Lopingian fossils. However, according to most recent published data (Gao et al., 2020), the Maokou Formation is Guadalupian (upper part of the Roadian – Capitanian). Therefore, I do not include these species, as well as the genus *Acanthophillipsia*, in the review of Lopingian trilobites, but I consider it necessary to mention this locality, the age of which may require clarification.

The fossil lists of the Changxing Formation of the Wenjiangsi Section of Guiding County indicate the presence of *Pseudophillipsia obtusicauda* (Kayser, 1883) and *Ditomopyge (Carniphillipsia) chongqingensis* (Lu, 1974), found in mudstones and cherts together with a variety of bivalves, brachiopods and rare cephalopods (Shen and He, 1994).

From the Changhsingian Dalong Formation in the Zhongying Section of Qinglong County, three new trilobite species described by Qian (1977) occur, namely *Pseudophillipsia qinglongensis* Qian, 1977, *Ditomopyge (Carniphillipsia) pyriformis* (Qian, 1977) and *Acropyge multisegmenta* Qian, 1977.

Guangxi Zhuang autonomous region. Based on finds of a well-preserved cephalon and pygidium found in the Lopingian of the Heshan Section, Qian (1977) described a new species of *Ditomopyge (Carniphillipsia) heshanensis* (Qian, 1977). This section exposes limestones of the Wuchiapingian Heshan Formation and the Changhsingian Talung Formation (Shen et al., 2007). The trilobite remains in question appear to come from the Heshan Formation.

Also, in the Guangxi, but much further east, in Laibin County, the Paoshui Section, also from the Heshan Formation, has yielded of *Pseudophillipsia obtusicauda* (Kayser, 1883) mentioned by Yang et al. (1987) and found in siliceous limestones together with bivalves and brachiopods.

Guangdong Province. *Pseudophillipsia obtusicauda* (Kayser, 1883) is known from the Changxing Formation in Qujiang County (Zhou, 1977). According to Kobayashi and Hamada (1984a), this find belongs to the species *Ditomopyge (Carniphillipsia) lui* (Kobayashi et Hamada, 1984a).

Jiangxi Province. From here Zhang (1982) described new species: *Pseudophillipsia shang-gaoensis* Zhang, 1982, the cranidium of which comes from the Laoshan Member (Loping Formation) in Shanggao County, and *Brachymetopus gaoanensis* Zhang, 1982 from similar deposits in another Gao'an County. According to modern data, the latter species is most likely a representative of *Cheiropyge*.

Northeast of the same province in the Mingshan Coalfield, the holotype of *Pseudophillipsia obtusicauda* (Kayser, 1883) comes from the Lopingian, discovered in red-gray limestone along with a rich assemblage of fossils represented by gastropods, bivalves, cephalopods, echinoderms, brachiopods and corals (Kayser, 1883). Northeast of Mingshan there is another locality with Lopingian trilobites (Zhang, 1982), from which *Pseudophillipsia obtusicauda* are also known (Kayser, 1883).

West Timor, Indonesia. Several fragmentary cephalons come from Permian in the vicinity of the Kupang City in the Amarassi region, on the basis of which Beyrich (1865) established a new species, *Phillipsia parvula* Beyrich, 1865. The locality near the Kupang City is known in the literature like Ajer Mati or Kali-Mati (Mount Tabeno), beds with fossils (corals, brachiopods, bryozoans, crinoids, etc.) represented by brown marls are called Amarassi Beds. These deposits, according to modern data, are of Wuchiapingian age based on the brachiopod assemblage (Archbold in Charlton et al., 2002, p. 741; Winkler Prins, 2008, p. 390). Species of *Phillipsia parvula* was previously tentatively assigned to the genus *Microphillipsia* (Hahn and Brauckmann, 1975) and then served as the type species for the establishment of the new genus *Timorcranium* (Brauckmann and Gröning, 2013).

Trilobites of the genus *Endops*, collected in the Permian of Timor from the Artinskian to the Wuchiapingian stages and located in the private collection of Dr. J. Savill, are indicated in Owens (2003, p. 383). However, there is no further detailed information on these finds.

Japan. In the western part of the country, in Gifu Prefecture, near the Akasaka Town, outcrops of Permian "Akasaka Limestone" are well known. From there, Kobayashi and Hamada (1984a; 1984b) described many species of trilobites, most

of which are Guadeloupian in age. However, from the upper part of the section belonging to the foraminiferal zone of *Reichelina changhsingensis*, they (1984b) described the cranidia and pygidia of a new species of *Pseudophillipsia (Nodiphillipsia) hanaokensis* Kobayashi and Hamada, 1984b.

The foraminiferal species *Reichelina changhsingensis* Sheng and Chang is the index fossil for the Lopingian (Ueno and Tsutsumi, 2009), and the deposits themselves, representing the Ichihashi Formation, are apparently Wuchiapingian (Kani et al., 2013).

In this work, I propose not to use the subgenus *Pseudophillipsia (Nodiphillipsia)*, see above, therefore I classify all its representatives as *Pseudophillipsia* (more on this in the section "remarks" on the genus *Pseudophillipsia*).

Thailand. In the northern part of the country, in the Lampang Province, several localities of Lopingian trilobites are located nearby: a small outcrop near the Huai Mae Phlung River and on the northern ridge of the Khao Doi Pha Phlung Mountains. Here from the Huai Thak Formation, represented by thick sequences of shales and sandstones (Waterhouse, 1983, p. 114), Kobayashi and Sakagami (1989) described several pygidia, identifying them as *Pseudophillipsia (Nodiphillipsia) aff. ozawai* Kobayashi et Hamada, 1984b. Horizons with trilobites contain fusulinids, incl. *Gallowayinella guidin-gensis* Liu, Xiao and Dong, indicating their Changhsingian (Ueno and Sakagami, 1991). Findings of *Pseudophillipsia (Nodiphillipsia) aff. ozawai* in Doi Pha Phlung have been noted elsewhere (Ishibashi, 1998).

New Zealand. An interesting locality of Lopingian fauna is found in New Zealand and is associated with a thick lens of pebble conglomerate in the upper part of Countess Formation on the Oreti River near Mossburn, a town in northern Southland. From there, a rich fossil assemblage was described, including brachiopods, bryozoans, crinoids, mollusks and trilobites (Hyden et al., 1982). The latter are represented by pygidium (Hyden et al., 1982, fig. 10), which, apparently, can be attributed to the *Triploetus*. Re-examination of the Countess Formation by Aitchison et al. (1988) allowed it to be assigned to the Stephens Subgroup and dated to the terminal Lopingian.

Spitsbergen. The northernmost locality of Lopingian trilobites in the world is located on the Ahlstrandhalvøya Peninsula of Spitsbergen Island. Here, thick deposits of the Kapp-Starostin Formation are exposed, in which trilobites were discovered, described by Kobayashi (1987) as a new

species *Neoproetus borealis* Kobayashi, 1987. The complete exoskeleton of *Neoproetus borealis* comes from the middle part of the formation (layers AP6), and two pygidia are from the upper part (layers AP9). According to Nakazawa (1999), these layers belong to its upper Hovtinden Member. According to modern data, the Kapp-Starostin Formation is of Kungurian (?) – Changhsingian age (Uchman et al., 2016) or Kungurian – Wuchia-pingian (Lee et al., 2022), and the age of the Hovtinden Member is most likely Lopingian (Shen, 2018).

From the lower part of the formation of the Svenskeegga member of Akseløya Island, located north of Ahlstrandhalvøya Peninsula, numerous remains of *Neoproetus borealis* Kobayashi, 1987 have also been described (Bruton, 1999).

The species *Neoproetus borealis* Kobayashi, 1987 was assigned by Owens (2003, p. 382) to the genus *Triporetus*, with which subsequent researchers agree (e.g., Fortey and Heward, 2015, p. 2015).

LOPINGIAN TRILOBITE GENERA AND THEIR MORPHOLOGY

Brachymetopus (Acutimetopus) Hahn and Hahn, 1985

The latest members of the *Brachymetopus* genus, originating in the Early Pennsylvanian and extinct throughout the Permian. The only Lopingian species, *Brachymetopus (Acutimetopus) caucasicus* Licharew in Weber, 1944, is known from a pygidium from the Changhsingian of the North Caucasus (Table 17).

Brachymetopus (Acutimetopus) has a subtriangular cephalon with an apical peak in the anterior part, which distinguishes them from all other subgenera of *Brachymetopus* and makes them more similar to the typically Permian genus *Cheiropyge*. The latter is believed to be an ancestor of the subgenus discussed here. This hypothesis was proposed by Hahn and Hahn in their study on phylogeny (1996).

The pygidia of *Brachymetopus (Acutimetopus)* are relatively highly segmented: the axis consists of more than 18 rings, and the lateral lobes have 6–7 pairs of pleural ribs, often ending in spines. More details about the diagnosis and comparison of this subgenus can be found in the systematic part of this article.

Cheiropyge Diener, 1897

Cheiropyge species occur exclusively in the Permian and are quite rare. They have a subtriangular cephalon and are similar in morphology to *Brachymetopus (Acutimetopus)*. Like most members of the family Brachymetopidae, the facial sutures of *Cheiropyge* are ankylosed. The glabella is conical, relatively swollen, lacking furrows and lobes, including and L₁-lobes. The pygidium is triangular in with a long, convex, strongly segmented axis, consisting of 13–20 rings. Six pairs of pleural ribs and an unpaired swollen terminal lobe behind the axis are present. On the surface of the pygidium, there are numerous tubercles of different sizes, the largest of which are variably located on some rings of the axis and anterior pleural ribs.

Cheiropyge differs from the closely related genus *Brachymetopus* in having larger eyes, the absence of genal spines and L₁-lobes of the glabella, as well as the main difference being in the presence of an unpaired terminal lobe behind the axis.

Perhaps due to its rarity, the history of research on this genus is somewhat confusing. *Cheiropyge* was established by a pygidium (Diener, 1897) found in the Lopingian of the Himalayas (Table 17). Almost half a century later, Weller (1944, p. 322) described the species of *Cheiropyge kansasensis* from the Upper Pennsylvanian of Kansas (the upper part of the Haskell Limestone), which at that time were considered Permian. Based on the similar morphology of this pygidium to *Ch. Himalayensis*, Weller attributed the species of *kansasensis* to *Cheiropyge* and also noted that he was the first to describe the cephalon and thorax of this genus, but the description of the pygidium, Weller did not include an image of it in his work, noting that it was poorly preserved.

Later, Kobayashi and Hamada (1982) established a new subgenus *Cheiropyge (Suturikephalion)* based on *Ch. koizumii*, the type series of which comes from the Permian (Capitanian) of Japan. They compared the cephalons of *Ch. koizumii* with the then known cephalons *Ch. kansasensis*, pointed out their similar morphology, but noted that *Ch. koizumii* has facial sutures that are absent in the holotype of *Ch. kansasensis*. The presence of facial sutures was, in principle, unusual for brachymetopines, in which these structures are fused.

Owens re-examined the type material of *Ch. kansasensis*, provided an image of the pygidium (Owens, 1983, pl. 5, fig. 18) and attributed this species to the genus *Brachymetopus*. Obviously, based on the absence of a terminal lobe, the shape

of the axis and the spines at the ends of the pleurae are not characteristic of *Cheiropyge*. A little later, Hahn and Hahn (1985) included *kansasensis* in the subgenus *Brachymetopus* (*Acutimetopus*).

Because of this confusion, many publications have based the diagnosis of *Cheiropyge* on the morphology of the cephalon of *Brachymetopus* (*Acutimetopus*) *kansasensis*, which is a member of a different genus. Therefore, for example, Maximova (1960, p. 140) indicated that *Cheiropyge* has L_1 -lobes, and the pygidial ends in spines on the pleurae.

Also, Hahn and Hahn (1985) noted that *Cheiropyge* (*Suturikephalion*) is a synonym for *Cheiropyge* and the presence of facial sutures in *Ch. koizumii*, which Kobayashi and Hamada described explaining the presence of these structures as taphonomical (post-mortem) changes to the cephalon.

In a later work, Kobayashi and Hamada (1984a, pl. 1, figs. 1, 2, 4) provided images of other specimens of *Cheiropyge koizumii*, on which the facial sutures were not visible. This has also been noted by other modern authors (Flick and Shiino, 2021), who studied the type material and new collections of *Ch. koizumii*. The latter pointed out that the facial sutures described by Kobayashi and Hamada (1982) look unnatural, located towards the anterior part of the glabella instead of running by the eyes. According to Flick and Shiino (2021), most specimens of *Ch. koizumii* do not have this feature. Accordingly, these structures can only be interpreted as postmortem structures that have no taxonomic significance.

It's interesting that another species of *Cheiropyge*? *gaoanensis*, described by Zhang (1982) from the Lopingian of China also has structures similar to facial sutures on the cephalon. However, Zhang himself does not mention this in the description. This led Hahn and Hahn (1996, p. 154) to believe that these structures were not postmortem features but a neotenic phenomenon. Which, apparently, based on the conclusion of Flick and Shiino (2021), is still incorrect.

The morphology of *Cheiropyge* (?) *gaoanensis* indicates its relation to *Cheiropyge*, but the pygidial pleurae end in short marginal spines, which differs from this species all other members of *Cheiropyge*. Therefore, following Flick and Shiino (2021), I tentatively classify *gaoanensis* as a member of *Cheiropyge*.

According to Hahn and Hahn (1996, p. 154) *Cheiropyge* originated from *Brachymetopus* (*Acutimetopus*) in the Early Permian. This is supported

by their shared common characteristics of these taxa: the triangular shape of the cephalon with a terminal apex (apical peak), six pairs of pleural ribs on the pygidium, as well as the presence of a seventh fused pair, which forms a terminal unpaired spine behind the pygidium in *B. (Acutimetopus)* and a terminal swollen lobe in *Cheiropyge*.

***Tripuroetus* Kobayashi and Hamada, 1979**

As a subgenus, *Neopuroetus* (*Tripuroetus*) was described by Kobayashi and Hamada (1979) based on the monotypic species *N. (T.) subovalis*, established by them, the type series of which came from the Cisuralian (Asselian) of northern Thailand. Later, Owens (1983, p. 17) noted that the morphology of *Neopuroetus* (*Tripuroetus*) differs from *Neopuroetus*, and is more similar to the genera *Paladin* and *Griffithides*. It was introduced as an independent genus *Tripuroetus* by Brezinski (1992), establishing in it three new species from the Cisuralian (Wolfcampian) of Texas, and also noting the shared characters of *Tripuroetus* with *Paladin* and *Ditomopyge*.

Fortey and Heward (2015) described in detail a new species, *Tripuroetus bonbon*, from the Permian (Kungurian–Roadian) of Oman. However, *Tripuroetus* was removed from *Ditomopyginae* and placed in the family *Proetidae* (without specifying a subfamily), since it lacks the typical glabellar morphology characteristic of *Ditomopyginae* and has a short pygidium with a small number of segments (both axial rings and pairs of pleural ribs).

Tripuroetus is characterized by a pear-shaped glabella with a very swollen anterior part. The small and teardrop-shaped L_1 -lobes are separated from the glabella. The posterior part of the glabella often has L_2 – L_4 lobes. The pygidium in *Tripuroetus* is elongated in width, short, has a wide convex axis, usually consisting of nine rings and 5–6 pleural ribs.

Lopingian members of *Tripuroetus* are known from Spitsbergen and occur in the Kapp Starostin Formation (Table 17). They were first established there by Kobayashi (1987), however, since the anterior part of the cephalon was not preserved on the type material, he did not specify the subgenus and described the new species as *Neopuroetus borelais* [sic!].

Later, using new and more complete material from the same formation of Spitsbergen, Bruton (1999) described these trilobites in detail, but assigned the species *borealis* to the subgenus *Paladin* (*Neokaskia*). This subgenus was considered

by Owens (2003, p. 383) to be synonymous with the genus *Tripoetus*.

Records of *Tripoetus* from Spitsbergen are not the only ones of this genus in the Lopingian. The pygidium (Hyden et al., 1982, fig. 10) with a morphology similar to *Tripoetus* comes from the Stephens Subgroup in the vicinity of Mossburn in New Zealand. Its outline and its convex axis with eight or nine rings, six pleural ribs, and distinct border allow us with some confidence to attribute this specimen to belong to this genus *Tripoetus*.

***Paraphillipsia* Toumansky, 1930**

This genus was established and described in detail (Toumansky 1930 and Tumanskaya 1935) based on specimens from the Guadalupian (Woardian) olistoliths of the Crimea. *Paraphillipsia* species occur throughout the Permian, but are most diverse in the Middle (Table 2).

Paraphillipsia has a distinctive morphology, different from most Permian genera. Its main characters include the presence of a large and very wide glabella, with a constriction in the central part. The L_1 -lobes are well defined and the narrow librigenae end in rounded genal angles. An important feature of *Paraphillipsia* is the broad and weakly segmented pygidium, with a wide axis consisting of 11 rings and lateral lobes, which usually bear 5–6 pairs of pleural ribs, passing into a pygidial border, devoid of a border furrow.

In the Lopingian, *Paraphillipsia* occurs in the Changhsingian of the North Caucasus and is represented by a new species, *P. urushtensis* sp. nov. – quite similar to *P. karpinskyi* Tumanskaya, 1935 from the Roadian olistoliths of Crimea. In addition to *P. urushtensis* sp. nov. the pygidium of *P. (?) middlemissi* is known, described by K. Diener (1897) from isolated blocks of Chitichun limestone in Tibet (Table 17). The latter species determined in open nomenclature is conditionally assigned to *Paraphillipsia*, but a more precise determination will be possible only after examination with the material, which should be stored in the Geological Survey of India (Calcutta) under number GSI 6069 (Hahn and Hahn, 2008, p 130). However, unfortunately, it was not possible to find out about its storage location.

***Kathwaia* Grant, 1966**

Kathwaia is known from represented in the Middle, Upper and possibly Lower Series of the Permian System. It was described by Grant (1966) based on the monotypic species *Kathwaia capitorosa* Grant, 1966, the holotype of which was repre-

sented by a single enrolled exoskeleton discovered in the Lopingian of Pakistan (Salt Range, near the Kathwai Village).

Members of *Kathwaia* are characterized by a highly swollen pear-shaped glabella that hangs vertically and overlaps the anterior border. The distinct teardrop-shaped L_1 -lobes are separated from the glabella by wide furrows. *Kathwaia*'s eyes are small. The most important feature of the members of the genus is that their exoskeleton is sculptured with numerous large tubercles, clearly visible on the cephalon. The pygidium is weakly segmented: the axis consists of 7–9 rings, pleural ribs – 6–9 pairs.

In total, very few records and species of *Kathwaia* are known (Table 6). In the Lopingian there are two of them – *K. capitorosa* Grant, 1966 and *K. caucasica* (Weber, 1944) from the North Caucasus. In the revision of this article, I consider *K. capitorosa* to be a junior subjective synonym of *K. caucasica*. Therefore, there is only one species, *Kathwaia caucasica*, in the Lopingian.

***Neogriffithides* Toumansky, 1930**

There are no reliable remains of the trilobite genus *Neogriffithides* known in the scientific literature. This is a fairly long-lived genus, occurring from the Middle Carboniferous (Moscovian) to the Middle Permian (Wordian). The latest representatives of this genus: *N. extremorientalis* Flick et Shino, 2021 from the Wordian of Japan, *N. siculus* (Gemmellaro, 1892) from Wordian of Sicily, *N. gemmellaro* Tumanskaya, 1935, *N. almensis* Tumanskaya, 1935 and *N. ismailensis* Tumanskaya, 1935 from the Roadian of Crimea. In July 2024, in the Russian Far East (Primorsky Krai, Nakhodka Reef Locality), scattered remains of trilobites were discovered, which I tentatively attribute to the *Neogriffithides*. More detailed information about this discovery should be published soon in separate articles.

***Timorcranium* Brauckmann and Gröning, 2013**

Timorcranium is characterized by a flask-shaped (slightly pear-shaped) glabella, slightly constricted in the middle part wider in the anterior than in the posterior. The glabella overlaps the anterior border border, and has three pairs of smooth lateral furrows. The fixigenae are very wide. *Timorcranium* is very small (cranidium 3.2 mm long) and appears to be the smallest Permian trilobite.

The only Lopingian species, *Timorcranium parvulum* Beyrich, 1865, comes from the Chang-

hsingian of West Timor (Table 17) and is represented by an incomplete cranium. It was redescribed in detail and conditionally assigned first to *Microphillipsia* by Hahn and Brauckmann (1975), and later Brauckmann and Gröning (2013) established a new genus *Timorcranium* for it, convincingly showing the differences from *Microphillipsia* and the subfamily Ditomopyginae.

Acropyge Qian, 1977

Typically, Guadalupian-Lopingian trilobites. *Acropyge* was described by Yu. Qian (1977) based on the then monotypic species *Acropyge multisegmenta* Qian, 1977, the type series of which came from the Changhsingian of China (Table 17).

Members of *Acropyge* have an inverted flask-shaped glabella, devoid of furrows. Behind the glabella there is a long median preoccipital lobe, and the preglabellar field is wide and depressed. The structure of the cranium of *Acropyge* is close to the genus *Ampulliglabella*. A particular difference between *Acropyge* and other Permian trilobites is the long subtriangular, highly segmented pygidium, the axis of which consists of 20–28 rings and the lateral lobes bears 12–14 pairs of pleural ribs. A postaxial ridge is usually present behind the axis, so the pygidium itself is peak-shaped.

Three species of *Acropyge* are known from the Lopingian: the type species *Acropyge multisegmenta* Qian, 1977, *A. brevica* Yin, 1978 from the Lopingian of China, and *A. weggeni* Hahn and Hahn, 1981 from the Lopingian of Iran. According to R. Lerosey-Aubril (2012, p. 9), *Acropyge weggeni* differs from the first two species in that it has a wider axis and a slightly different arrangement of pleural ribs, the posterior pairs of which are located almost subparallel to the axis (Figure 12).

Ditomopyge (Carniphillipsia) Hahn and Brauckmann, 1975

This subgenus, which ranges from the Pennsylvanian until the end of the Lopingian, is one of the longest-living Carboniferous and Permian protetids. It was established by Hahn and Brauckmann (1975) as a subgenus of *Pseudophillipsia* (*Carniphillipsia*) with the type species *Ps. ogivalis* (Gauri, 1965) from the Upper Pennsylvanian of the Carnic Alps (Austria).

Ditomopyge (*Carniphillipsia*) is apparently a transitional form between the genera *Ditomopyge* and *Pseudophillipsia*, and therefore bears many of the common characteristics of them. The cephalon resembles that of *Pseudophillipsia*: there are medial and lateral preoccipital lobes, but the gla-

bellar furrows are weakly expressed or, more often, absent, which makes it similar to *Ditomopyge*. Some species of *Ditomopyge* (*Carniphillipsia*) have laterally depressed areas on the glabella, therefore the species of the subgenus can be divided into three groups, having a glabella devoid of furrows and depressions, a glabella with depressions, and a glabella with small furrows (Figure 9).

The pygidium more closely resembles that of *Ditomopyge* and is somewhat less segmented than that of *Pseudophillipsia*, with an average of 17–21 axial rings and 9–13 pleural ribs. However, in some species the number of axial rings can reach up to 25, and pairs of pleural ribs – up to 15 (Table 18).

Among the Lopingian trilobites, five species of this subgenus are reliably known (Table 18). One of them, *D. (C.) fatmii* Grant, 1966, comes from the Wuchiapingian of Pakistan. The remaining species are confined to the Lopingian of China: *D. (C.) chongqingensis* occurs in a number of localities of Changhsingian in Southern China; *D. (C.) heshanensis* (Qian, 1977) is known from the Changhsingian of Guizhou; *D. (C.) pyriformis* from the Changhsingian of Guizhou; *D. (C.) lui* – from the Changhsingian of Chongqing; *D. (C.) raggyorkaensis* (Qian, 1981) from the Changhsingian of Tibet.

A detailed comparison of these species is discussed in the work of Lerosey-Aubril and Angiolini (2009). Abbreviated information is provided here along with reconstructions (Table 18; Figure 9).

Pseudophillipsia Gemmellaro, 1892

The most widespread and typical of Lopingian trilobites. Its oldest members are known from the Pennsylvanian and, apparently, separated from *Ditomopyge* (*Carniphillipsia*) in that epoch. The main feature of the morphology of *Pseudophillipsia* is the lateral and medial preoccipital lobes isolated from the glabella, forming a “festoon” structure, convex glabellar lobes (L₂–L₄), genal spines, as well as an elongated pygidium, oval-triangular in shape, having a highly segmented axis (20–27 rings) and many pleural ribs (13–17). More about the genus diagnosis and comparison in the corresponding section.

In the Lopingian, the species diversity of *Pseudophillipsia* is the highest among species of other genera (Table 19) and amounts to 47% (Figure 13). Of these, in seven species the structure of the cephalon, namely the glabella, is known, according to which they can be quite confidently attributed to the genus *Pseudophillipsia*. Four of them are described from China.

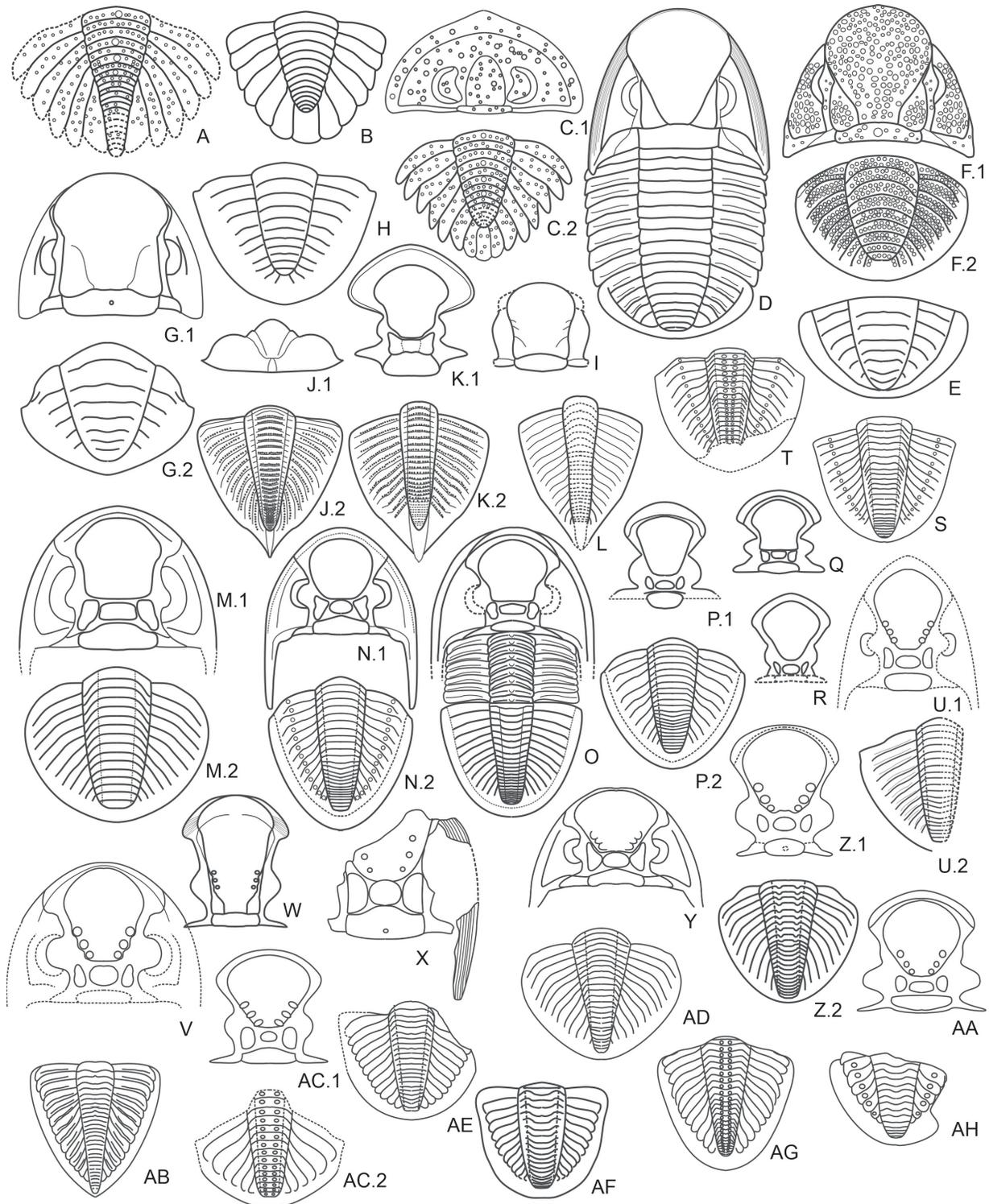


FIGURE 12 (caption on next page).

Thus, *Pseudophillipsia anshunensis* Qian, 1977, represented by a cephalon and pygidium, comes from the Wuchiapingian of the Guizhou province. Cephalon *Ps. anshunensis* is relatively

narrow, and the glabella greatly widens towards the anterior part. In front of it, as far as can be judged from the photograph (Qian, 1977, pl. I, figs. 4), there is a wide preglabellar field, and in the pos-

FIGURE 12 (figure on previous page). Schematic reconstructions of all known species and species determined in open nomenclature of the Lopingian trilobites. **A** – *Brachymetopus (Acutimetopus) caucasicus* Licharew in Weber, 1944, pygidium, Changhsingian of North Caucasus; **B** – *Cheiropyge himalayensis* Diener, 1897, pygidium, Wuchiapingian (?) of Tibet; **C** – *Ch. (?) gaoanensis* (Zhang, 1982), cephalon (**C.1**) and pygidium (**C.2**), Wuchiapingian of Southern China; **D** – *Triproetus borealis* Kobayashi, 1987, complete exoskeleton, Lopingian of Spitsbergen; **E** – *Tr. sp.*, pygidium, Changhsingian (?) of New Zealand; **F** – *Kathwaia caucasica* (Weber, 1944), cephalon (**F.1**) and pygidium (**F.2**), Lopingian of North Caucasus and Pakistan; **G** – *Paraphillipsia urushtensis* sp. nov., cephalon (**G.1**) and pygidium (**G.2**), Changhsingian of North Caucasus; **H** – *Par. (?) middlemissi* Diener, 1897, pygidium, Wuchiapingian (?) of Tibet; **I** – *Timorcranium parvulum* (Beyrich, 1865), cranidium, Wuchiapingian of Timor; **J** – *Acropyge weggeni* Hahn et Hahn, 1981, pygidium posteriorly (**J.1**) and superiorly (**J.2**), Lopingian of Iran; **K** – *Ac. brevica* Yin, 1978, cranidium (**K.1**) and pygidium (**K.2**), Changhsingian of Southern China; **L** – *Ac. multisegmenta* Yin, 1978, pygidium, Changhsingian of Southern China; **M** – *Ditomopyge (Carniphillipsia) fatmii* Grant, 1966, cephalon (**M.1**) and pygidium (**M.2**), Wuchiapingian of Pakistan; **N** – *Dit. (C.) chongqingensis* (Lu, 1974), cephalon (**N.1**) and pygidium (**N.2**), Changhsingian of Southern China; **O** – *Dit. (C.) heshanensis* (Qian, 1977), complete exoskeleton, Wuchiapingian of Southern China; **P** – *Dit. (C.) lui* (Kobayashi et Hamada, 1984a), cranidium (**P.1**) and pygidium (**P.2**), Wuchiapingian of Southern China; **Q** – *Dit. (C.) raggyorcaensis* (Qian, 1981), cranidium, Changhsingian of Tibet; **R** – *Dit. (C.) pyriformis* (Qian, 1977), cranidium, Changhsingian of Southern China; **S** – *Pseudophillipsia (?) hungarica* (Schréter, 1948), pygidium, Changhsingian of Hungary; **T** – *Ps. (?) cf. hungarica* (Schréter, 1948), pygidium, Changhsingian of Slovenia; **U** – *Ps. anshunensis* Qian, 1977, cephalon (**U.1**) and pygidium (**U.2**), Wuchiapingian of Southern China; **V** – *Ps. solida* Weber, 1944, cephalon, Changhsingian of North Caucasus; **W** – *Ps. solida* Weber, 1944, cranidium, Changhsingian of Slovenia; **X** – *Ps. n. sp., aff. sumatrensis* (Roemer, 1880), cephalon, Changhsingian of Slovenia; **Y** – *Ps. qinglongensis* Qian, 1977, cephalon, Changhsingian of Southern China; **Z** – *Ps. hanaokensis* Kobayashi et Hamada, 1984b, cranidium (**Z.1**) and pygidium (**Z.2**), Lopingian of Japan; **AA** – *Ps. shanggaensis* Zhang, 1982, cranidium, Wuchiapingian of Southern China; **AB** – *Ps. (?) aff. ozawai* Kobayashi et Hamada, 1984b, pygidium, Changhsingian of Thailand; **AC** – *Ps. obtusicauda* (Kayser, 1883), cranidium (**AC.1**) and pygidium (**AC.2**), Lopingian of Southern China; **AD** – *Ps. (?) subcircularis* Qian, 1977, pygidium, Wuchiapingian of Southern China; **AE** – *Ps. (?) cf. mustafensis* Tumanskaya, 1935, pygidium, Changhsingian of North Caucasus; **AF** – *Ps. (?) parvizii* Lerosey-Aubril, 2012, pygidium, Wuchiapingian of Iran; **AG** – *Ps. (?) caucasica* Weber, 1944, pygidium, Changhsingian of North Caucasus; **AH** – *Ps. (?) aff. caucasica* Weber, 1944, Lopingian of Iran.

terior part of the glabella there are three pairs of distinct L₂–L₄ lobes.

Another species, *Pseudophillipsia qinglongensis* Qian, 1977, described from Changhsingian of the same province, is represented by an almost complete exoskeleton, but the lower part of its pygidium is broken off. From *Ps. anshunensis* differs by a wider cephalon, larger preoccipital lobes (both lateral and medial), and, apparently, a smaller preglabellar field.

Pseudophillipsia shanggaensis Zhang, 1982, described from its cranidium, comes from the Wuchiapingian of Jiangxi Province. Its characteristic feature is its protruding palpebral lobes. However, its preservation, represented by a cast, does not allow, in my opinion, to strongly distinguish it from another widespread species in the Lopingian of China – *Pseudophillipsia obtusicauda* (Kayser, 1883), recorded from a number of Lopingian (both Wuchiapingian and Changhsingian) deposits of South China.

TABLE 18. Lopingian species of *Ditomopyge (Carniphillipsia)*.

Species	Images	Part	Axial rings	Pleural ribs
<i>D. (C.) fatmii</i> Grant, 1966	Grant 1966, pl. 13, fig. 2,4; herein – Figures 12M.1, 12M.2	Cc	17	12
<i>D. (C.) chongqingensis</i> (Lu, 1974)	Lu, 1974, pl. 166, figs. 27,28; Lerosey-Aubril, 2012, fig. 6 d, g, h, k, m, p; herein – Figures 12N.1, 12N.2	Cph, Py	25	14–15
<i>D. (C.) heshanensis</i> (Qian, 1977)	Qian, 1977, pl. 1, fig. 10 herein – Figure 12O	Cc	21	13–14
<i>D. (C.) pyriformis</i> (Qian, 1977)	Qian, 1977, pl. 1, fig. 10; herein – Figure 12R (only cranidium)	Cph	?	?
<i>D. (C.) raggyorcaensis</i> (Qian, 1981)	Qian, 1981, pl. 1, figs. 5,6; herein – Figure 12Q (only cranidium)	Cr, Py	20	12
<i>D. (C.) lui</i> (Kobayashi et Hamada, 1984a)	Lu, 1974, pl. 166, figs. 25,26; herein – Figure 12P	Cr, Th+Py	22–23	13–14

TABLE 19. Lopingian species of *Pseudophillipsia*.

Species	Images	Part	Axial rings	Pleural ribs
<i>Ps. anshunensis</i> Qian, 1977	Qian, 1977, pl. I, figs. 4,5; herein – Figure 12U.1, 12U.2	Cph, Py	22	12 (13–14)
<i>Ps. qinglongensis</i> Qian, 1977	Qian, 1977, pl. I, figs. 1–3; herein – Figure 12Y(only cephalon)	Cph, Th, Py*	?	?
<i>Ps. shanggaoensis</i> Zhang, 1982	Zhang, 1982, pl. 125, fig. 2; herein – Figure 12AA	Cr	?	?
<i>Ps. obtusicauda</i> (Kayser, 1883)	Zhang, 1982, pl. 125, fig. 1; herein – Figures 12AC.1, 12AC.2	Cc	20	12
<i>Ps. hanaokensis</i> Kobayashi et Hamada, 1984b	Kobayashi and Hamada, 1984a, pl. X, figs. 1-5; pl. XI, figs. 3,4; Text-fig. 6-a; Kobayashi and Hamada, 1984b, Figure 5; herein – Figure 12Z.1, 12Z.2	Cr, Py	25–24	10–11
<i>Ps. n. sp., aff. sumatrensis</i> (Roemer, 1880)	Hahn et al., 1970, Taf. 1, fig. 7, abb. 4; herein – Figure 9.24	*Cph, *Py	?	~12(?)
<i>Ps. solida</i> Weber, 1944	Weber, pl. II, fig. 8,9; herein – Figures 10 a–d, 12V, 12W	Cph	?	?
<i>Ps. (?) aff. ozawai</i> Kobayashi et Hamada, 1984b	Kobayashi and Sakagami, 1989, fig. 1; herein – Figure 12AB	Py	25–24	17
<i>Ps. (?) hungarica</i> (Schréter, 1948)	Schréter, 1948, fig. 4; Detre, 1991, figs. 2,3; herein – Figure 12S	Py	27	13
<i>Ps. (?) cf. hungarica</i> (Schréter, 1948)	Hahn et al., 1970, fig. 3; herein – Figure 12T	Py	>18	12(13–14)
<i>Ps. (?) parvizii</i> Lerosey-Aubril, 2012	Lerosey-Aubril, 2012, fig. 5; herein – Figure 12AF	Py	21	13
<i>Ps. (?) subcircularis</i> Qian, 1977	Qian, 1977, pl. I, figs. 7,8; herein – Figure 12AD	Py	23–24	12
<i>Ps. (?) caucasica</i> Weber, 1944	Weber, 1944, pl. II, fig. 4; herein – Figures 10 a–d, 12AG	Py	25	11
<i>Ps. (?) aff. caucasica</i> Weber, 1944	Lerosey-Aubril, 2012, figs. 4g–j, l, m; herein – Figure 12AH	Py	>17 (21–22)	10 (?)
<i>Ps. (?) cf. mustafensis</i> Tumanskaya, 1935	Weber, 1944, pl. II, fig. 3; herein – Figures 10 i–k, 12AE	Py	25	12

One species, *Pseudophillipsia hanaokensis* Kobayashi et Hamada, 1984b, is described from the Lopingian of Japan, and its type series consists of cranidia and pygidia. It is characterized by a swollen exoskeleton, small preoccipital lobes and a narrow occipital ring.

From the Changhsingian of Slovenia comes the *Pseudophillipsia* n. sp., aff. *sumatrensis* (Roemer, 1880), represented by an incomplete cephalon with pygidium. The cephalon partially preserves the cranidium and part of the librigena. Based on similar characters, Hahn et al. (1970) considered it close to the type species *Pseudophillipsia sumatrensis* (Roemer, 1880), described from the Guadalupian of Indonesia. It is worth noting that a very wide occipital ring and rather large preoccipital lobes greatly distinguish the Slovenian species determined in open nomenclature from other Lopingian trilobites, however, the

fragmentary of the material does not allow it to be compared in detail either with the type species or to describe a new one.

The species, *Pseudophillipsia solida* Weber, 1944, is described from Changhsingian of the North Caucasus and is discussed in detail in this article. The cranidium assigned to this species by Hahn et al. (1970) comes from Changhsingian of Slovenia.

Some species and species determined in open nomenclature are known only from pygidia, so in this article they are conditionally classified as *Pseudophillipsia*. Since we do not know the structure of their cephalata, especially the glabella, we can assume that they may be members of the related *Ditomopyge* (*Carniphillipsia*). Thus, from the Changhsingian of Thailand come pygidia identified by Kobayashi (Kobayashi and Sakagami, 1989) as *Pseudophillipsia* (*Nodiphillipsia*) aff. *oza-*

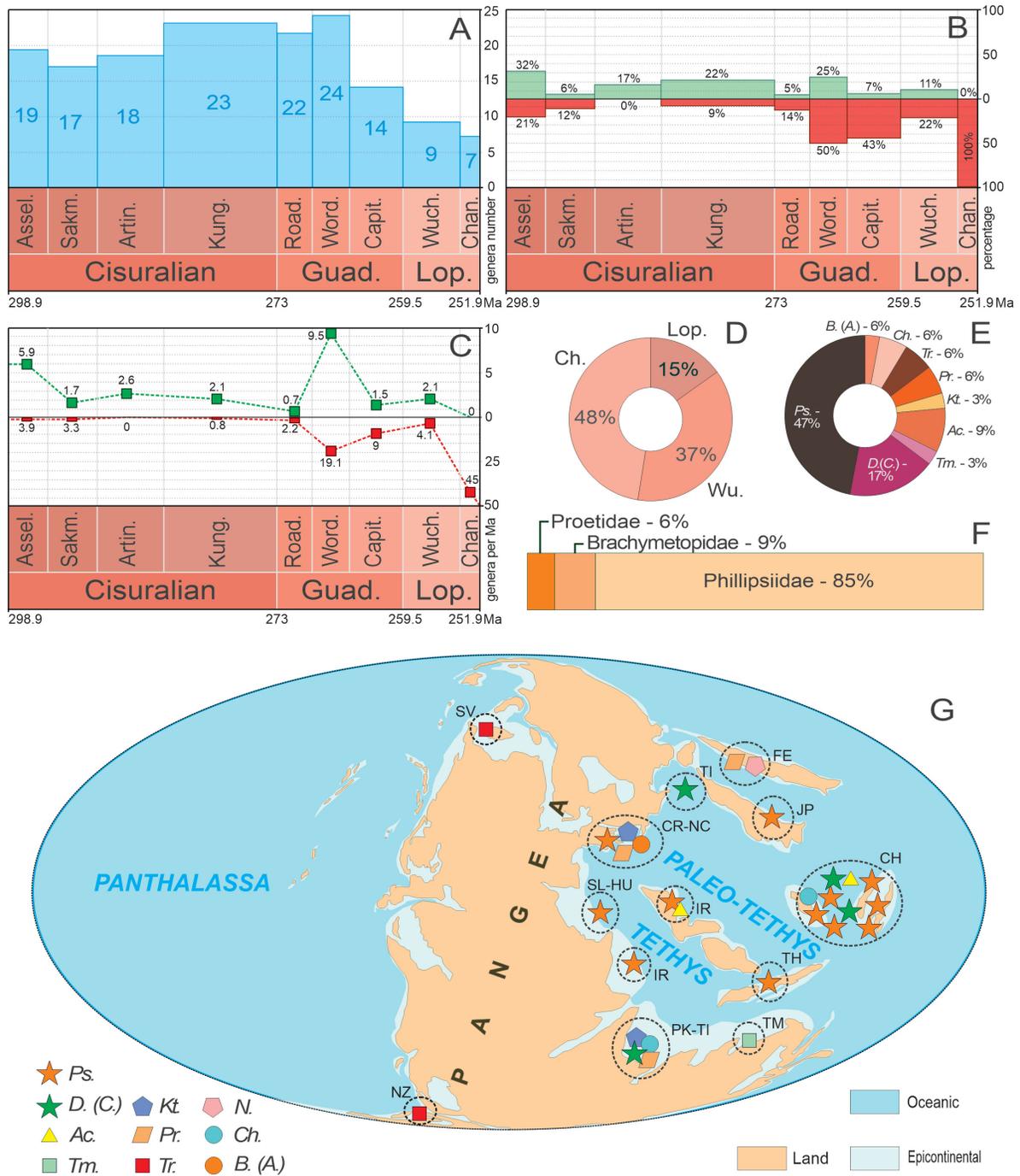


FIGURE 13. Infographics for this article. **A** – diversity of trilobite genera during the Permian; **B** – levels of origination (green bars) and extinction (red bars) of trilobite genera during the Permian; **C** – rates of origination (green curve) and extinction (red curve) of trilobite genera during the Permian; **D** – percentage of known Lopingian trilobite species; **E** – percentage of the number of species within the genera of Lopingian trilobites; **F** – percentage of Lopingian trilobite genera within families; **G** – trilobite genera on the palaeogeographic map of the world in the Lopingian (according to Blakey, 2016 with modifications and additions). Abbreviations: Wu – Wuchiapingian; Ch – Changhsingian; Lop – Lopingian without specifying the stage; SV – Spitsbergen; SL – Slovenia; HU – Hungary; CR – Crimea; NC – North Caucasus; FE – Far East; IR – Iran; PK – Pakistan; TI – Tibet; CH – Southern China; TH – Thailand; JP – Japan; TM – Timor; NZ – New Zealand; *Ps* – *Pseudophillipsia*; *D. (C.)* – *Ditomopyge (Carniphillipsia)*; *Ac* – *Acropyge*; *Tm* – *Timorcranium*; *Kt* – *Kathwaia*; *N* – *Neogriffithides* (?); *Pr* – *Paraphillipsia*; *Tr* – *Triporetus*; *Ch* – *Cheiropyge*; *B. (A.)* – *Brachymetopus (Acutimetopus)*.

wai Kobayashi et Hamada, 1984b. Indeed, the general shape of these pygidia, the border furrow, the convexity of the lateral lobes and the number of pleural ribs are consistent with those of *Pseudophillipsia ozawai* Kobayashi et Hamada, 1984b from the Capitanian of Japan (see: Kobayashi and Hamada, 1984a, pl. IX, figs. 4,5). However, Thai pygidia are somewhat narrower, have a narrower axis and a greater number of axial rings (up to 27). One of them (Kobayashi and Sakagami, 1989, fig. 1 a) has a somewhat peaked shape, which makes it similar to *Acropyge*, although the posterior part of the pygidium is not preserved, and this shape is possibly only a consequence of taphonomic deformation. I very tentatively assign these pygidia to the genus *Pseudophillipsia* (as well as to the species *Pseudophillipsia ozawai*).

The species *Pseudophillipsia* (?) *hungarica*, described by Schr ter (1948) based on pygidia, is known from Changhsingian of Hungary. A peculiarity of this species is the presence of a large tubercle at the geniculate bend of each pleural rib. Unfortunately, for *Ps.* (?) *hungarica*, no cephalae are described, which in all likelihood are known from there, since Detre (1991) reported significant collections of these trilobites. A similar species to *Ps.* (?) *hungarica* was described by Hahn et al. (1970) from the Changhsingian of Slovenia.

The pygidium *Ps.* (?) *parvizii* Lerosey-Aubril, 2012 comes from the Wuchiapingian of Iran and have rather unusual morphology: its wide pygidial border widens significantly towards the rear. A similar structure is characteristic of the Late Pennsylvanian and Cisuralian species of *Ditomopyge*. This is also reported by the author (Lerosey-Aubril, 2012, p. 13), comparing the Iranian pygidium with the Cisuralian *Ditomopyge* (*Carniphillipsia*) *rotunda* Hahn and Hahn in Hahn, Hahn and Ramov s, 1990. Its closeness to *Ditomopyge* (*Carniphillipsia*) is also indicated by the number of pygidial segments (*Ps.* (?) *parvizii* has 21 axial rings and 13 pairs of pleural ribs), and Lerosey-Aubril (2012) classified *parvizii* as belonging to the *Pseudophillipsia* in the broad sense (*sensu lato*). Following Lerosey-Aubril (2012), I also classify this species tentatively as *Pseudophillipsia* and hope for new finds of cephalae from the Dalan Formation of the Zagros Mountains.

In the blocks on the Alma River in Crimea Tumanskaya (1935, p. 10) discovered difficult-to-identify remains of trilobites, which she described as species determined in open nomenclature of *Neogriffithides* sp. ind. No. 1 (block C), *N.* (?) sp. ind. No. 2 (block A) and *Pseudophillipsia* sp. ind. No. 1 (block B). The first two are represented by

incomplete poorly preserved pygidia. It is worth noting that Tumanskaya (1935) described the genus *Neogriffithides* and its species without complete exoskeletons, and associated the highly segmented pygidia of *Pseudophillipsia* with them. It was later noted (Ruggieri, 1959, p. 4; Owens, 1983, p. 18; Hahn and Hahn, 2015, p. 113–114) that members of *Neogriffithides* actually have a weakly segmented pygidium. I associate the remains of trilobites from blocks on the Alma River, identified by Tumanskaya as *Neogriffithides*, rather with both *Pseudophillipsia* and *Ditomopyge* (*Carniphillipsia*) due to their highly segmentation.

Pseudophillipsia sp. ind. No. 1, known by its incomplete pygidium, has a large number of axial rings (probably 25–26) and 11 pleural ribs obliquely descending to the posterior end, which, according to Tumanskaya (1935, p. 28) and Hahn et al. (1970, p. 317) relate it more closely to the genus *Anisopyge*. However, finds of the *Anisopyge* are limited to the Cisuralian and Guadalupian of North America (Owens, 2003, p. 381). Therefore, based on fragmentary material, I conditionally classify this species determined in open nomenclature as *Pseudophillipsia*.

The species *Pseudophillipsia* (?) *subcircularis* Qian, 1977, represented by a pygidium with 23–24 axial rings and 12 pairs of pleural ribs, is described from the Wuchiapingian of Guizhou (Qian, 1977, p. 283). Other finds are also known from the Lopingian of Southern China, usually pygidia, considered in this article as *Pseudophillipsia* (?) sp.

Herein, details are given of the pygidia of the species *Pseudophillipsia* (?) cf. *mustafensis* Tumanskaya, 1935 and *Pseudophillipsia* (?) *caucasica* Weber, 1944, known from the Changhsingian of the North Caucasus. *Pseudophillipsia* (?) aff. *caucasica* Weber, 1944 was described from the Lopingian of Iran. Its differences from the North Caucasian species are given in the section notes on the species *Pseudophillipsia* (?) *caucasica* Weber, 1944.

DISCUSSION

Taxonomically, Lopingian trilobites were relatively poorly represented (Table 20, Figure 13D–F). At the family level (Figure 13F), the majority of the species were classified as Phillipsiidae (85%), with Brachymetopidae and Proetidae accounted for 9% and 6%, respectively. Approximately the same proportion of trilobite families was present throughout the Permian. The distribution of species (and species determined in open nomenclature) of known

TABLE 20. Taxonomy of Lopingian trilobites adopted in this article. *primary identifications of unpublished trilobites from the Wuchiapingian of the Russian Far East.

Brachymetopidae Prantl et Přibyl, 1950
<i>Brachymetopus</i> McCoy, 1847
<i>Brachymetopus (Acutimetopus)</i> Hahn et Hahn, 1985
<i>Brachymetopus (Acutimetopus) caucasicus</i> Licharew in Weber, 1944
<i>Cheiropyge</i> Diener, 1897
<i>Cheiropyge himalayensis</i> Diener, 1897
<i>Cheiropyge</i> (?) <i>gaoanensis</i> (Zhang, 1982)
Proetidae Hawle et Corda, 1847
<i>Triproetus</i> Kobayashi and Hamada, 1979
<i>Triproetus borealis</i> Kobayashi, 1987
<i>Triproetus</i> sp.
Phillipsiidae Oehlert, 1886
Cummingellinae Hahn et Hahn, 1967
<i>Paraphillipsia</i> Toumansky, 1930
<i>Paraphillipsia urushtensis</i> sp. nov.
<i>Paraphillipsia</i> (?) <i>middlemissi</i> Diener, 1897
<i>Paraphillipsia</i> sp.*
<i>Timorcranium</i> Brauckmann et Gröning, 2013
<i>Timorcranium parvulum</i> (Beyrich, 1865)
Bollandiinae Hahn et Brauckmann, 1988
<i>Kathwaia</i> Grant, 1966
<i>Kathwaia caucasica</i> (Weber, 1944)
<i>Neogriffithides</i> Toumansky, 1930
<i>Neogriffithides</i> (?) sp.*
Ditomopyginae Hupé, 1953
<i>Acropyge</i> Qian, 1977
<i>Acropyge brevica</i> Yin, 1978
<i>Acropyge multisegmenta</i> Qian, 1977
<i>Acropyge weggeni</i> Hahn et Hahn, 1981
<i>Ditomopyge</i> Newell, 1931
<i>Ditomopyge (Carniphillipsia)</i> Hahn et Brauckmann, 1975
<i>Ditomopyge (Carniphillipsia) fatmii</i> Grant, 1966
<i>Ditomopyge (Carniphillipsia) chongqingensis</i> (Lu, 1974)
<i>Ditomopyge (Carniphillipsia) heshanensis</i> (Qian, 1977)
<i>Ditomopyge (Carniphillipsia) pyriformis</i> (Qian, 1977)
<i>Ditomopyge (Carniphillipsia) raggyorcaensis</i> (Qian, 1981)
<i>Ditomopyge (Carniphillipsia) lui</i> (Kobayashi et Hamada, 1984a)
<i>Pseudophillipsia</i> Gemmellar, 1892
<i>Pseudophillipsia anshunensis</i> Qian, 1977
<i>Pseudophillipsia hanaokensis</i> Kobayashi et Hamada, 1984b
<i>Pseudophillipsia</i> n. sp., aff. <i>sumatrensis</i> (Roemer, 1880)
<i>Pseudophillipsia obtusicauda</i> (Kayser, 1883)
<i>Pseudophillipsia qinglongensis</i> Qian, 1977
<i>Pseudophillipsia shanggaoensis</i> Zhang, 1982

TABLE 20 (continued).

<i>Pseudophillipsia solida</i> Weber, 1944
<i>Pseudophillipsia</i> (?) aff. <i>ozawai</i> Kobayashi et Hamada, 1984b
<i>Pseudophillipsia</i> (?) <i>caucasica</i> Weber, 1944
<i>Pseudophillipsia</i> (?) cf. <i>mustafensis</i> Tumanskaya, 1935
<i>Pseudophillipsia</i> (?) aff. <i>caucasica</i> Weber, 1944
<i>Pseudophillipsia</i> (?) <i>parvizii</i> Lerosey-Aubril, 2012
<i>Pseudophillipsia</i> (?) <i>hungarica</i> (Schréter, 1948)
<i>Pseudophillipsia</i> (?) cf. <i>hungarica</i> (Schréter, 1948)
<i>Pseudophillipsia</i> (?) <i>subcircularis</i> Qian, 1977
<i>Pseudophillipsia</i> (?) sp.

Lopingian trilobites (Figure 13E) suggests that most of them belonged to the two closely related *Pseudophillipsia* and *Ditomopyge* (*Carniphillipsia*). Almost half (47%) of the known species of Lopingian trilobites belong to the first genus; almost three times fewer (17%) belong to the second. Species of the *Acropyge* accounted for 9%. Other species and varieties are much less commonly found. So *Brachymetopus* (*Acutimetopus*), *Cheiropyge*, *Tripuroetus* and *Paraphillipsia* make up 6% of the total number of species, and *Kathwaia* and *Timorcranium* account for 3%, as they are represented only by only one species each.

Compared to the Guadalupian diversity, the Lopingian trilobites has lost several genera, which became extinct during the Wordian–Capitanian (Figure 13A). In particular, members of 17 genera are not known to survive into the Lopingian: *Hildaphillipsia*, *Neogriffithides*, *Neoproetus*, *Acanthophillipsia*, *Ampulliglabella*, *Anisopyge*, *Delaria*, *Ditomopyge* (*Ditomopyge*), *Endops*, *Jimbokranion*, *Microphillipsia*, *Novoameura*, *Permoproetus*, *Timoraspis*, *Doublatia*, *Nipponaspis* and *Weania*. Additionally, in the Wuchiapingian only one genus was recorded that was absent from the Guadalupian – *Timorcranium*. This is more likely due to the incomplete fossil record than the appearance of this genus during the Lopingian Epoch.

The distribution of Lopingian trilobites across stages (Figure 13D) shows the highest diversity in the Changhsingian, with 48%, and in the Wuchiapingian with only 37%. Lopingian trilobites, which are found in deposits that could not be reliably dated to a specific stage, account for approximately 15%. Here, it's worth noting that most of the Lopingian sections, from which trilobites originate, require more detailed stratigraphical clarification. And the figures presented here should not be interpreted as a basis for concluding that trilobite diver-

sity increased in the Changhsingian relative to the Wuchiapingian. In fact, we observe another distortion in the sample from more studied sections.

The palaeobiogeographic distribution of Lopingian trilobites has decreased compared to the previous epochs of the Permian and the Carboniferous, but it is not limited to only a few areas. The first striking change (Figure 13G) is the disappearance of trilobites from the western edge of the Mid-continent, which lived on the Panthalassa shelf. The trilobite fauna of this region, which was widespread in the Guadalupian, was quite endemic. Their genera were not found in Tethyan regions. The palaeobiogeographic areas of the Guadalupian trilobite fauna, noted by various researchers (Owens and Hahn, 1993; Brezinski, 2023) were very endemic (genera *Delaria*, *Novoameura*, *Anisopyge* and *Vidria*) and confined to subequatorial latitudes.

However, trilobite faunas associated with Panthalassa during the Lopingian seem to have been preserved in mid-latitudes in both hemispheres. (Figure 13G). This is confirmed by the discovery of Lopingian trilobite in Spitsbergen and New Zealand. It is possible that these palaeogeographic regions were refugia for some trilobite populations, where they were able to survive. It is equally curious that they are represented only by one genus, *Tripuroetus*. In comparison with the Tethyan trilobite fauna of the Lopingian, this genus is very rare. The lack of obvious marine connections to the Palaeo-Tethys can be explained by the absence of typical Tethyan genera in the mid latitudes of Panthalassa, as well as by the lack of *Tripuroetus* in the Tethyan areas.

The Tethys and Palaeo-Tethys margins continued to be rich in trilobite faunas. The main component of these faunas was *Pseudophillipsia* (Figure 13G), which was found in almost all

Lopingian Tethyan deposits. The closely related *Ditomopyge* (*Carniphillipsia*), which lived mainly in the eastern and northern parts of the Palaeo-Tethys and the southern Tethys oceans, but was absent from the western parts of both oceans, had a slightly less widespread distribution. Palaeo-Tethys also features the presence of a third species of the subfamily Ditomopyginae – *Acropyge*. This genus is restricted to southern China and northern Iran.

Similar Lopingian trilobite assemblages lived on both sides of the equator in the northwestern Palaeo-Tethys and the southern Tethys. The presence of these common assemblages is evidenced by the presence of the *Kathwaia* and *Paraphillipsia*, as well as *Cheiropyge* and *Brachymetopus* (*Acutimetopus*). The only genus that was not found in other Tethyan areas, *Timorcranium*, lived in the southeastern part of the Tethys.

Apparently, *Pseudophillipsia* and *Ditomopyge* (*Carniphillipsia*) were cosmopolitan and fairly successful trilobites from the Lopingian, surviving and until close to the major Permian-Triassic extinction events.

The Lopingian deposits of a pre-boreal sea basin, the Zechstein, located on the East European Platform, also lack trilobite remains. This can be attributed to hypersalinity and aridity. However, Zechstein deposits contain reef facies (Raczyński and Biernacka, 2014), as well as arthropod finds, including and cyclidans (Schweitzer et al., 2020, p. 279), which shared a similar lifestyle to trilobites.

During the Permian, the diversity of trilobites was represented by only one order (Proetida), three families (Brachymetopidae, Proetidae and Phillipsiidae) and about 38 genera (see supplements), which is extremely low compared to previous periods of the Palaeozoic. As is clearly evident from the presented graph (Figure 13A), throughout the three ages of the Cisuralian, the number of genera remained approximately constant (17–19), but in the Kungurian age it began to increase and reached 23 genera. The next surge in diversity was confined to the Wordian age of Guadalupian, when the number of genera increased to 24, and the level and rate of originations of new genera reached 25% and 9.5 (genera per Ma) respectively (Figure 13B, C). However, the second half of the Guadalupian is also characterized by a significant decrease in diversity: in the Wordian, the level of extinction of genera reached 50% and in the Capitanian – 43%. A high rate of extinction was noted during the Wordian (~19 genera per one Ma).

Apparently, the Late Guadalupian reduction in generic diversity can be linked to the Guadalupian mass extinction event, which has been noted by many researchers (e.g., Rampino and Shen, 2019). According to some researchers, this extinction event may be associated with eruptions from the Emeishan Large Igneous Province. This is evident not only through basaltic formations, but also through other geochemical anomalies (Bond et al., 2010; Ling et al., 2023). According to recent research, there may have been two mass extinction events during the Capitanian Age (Song et al., 2023). However, the largest reduction in trilobite genera (Figure 13B) is not confined to the Capitanian, but also to the Wordian.

Apparently, trilobite faunas were unable to recover after the Guadalupian extinctions and, throughout the Lopingian, lived out their last epoch of their existence. In the Lopingian, the only origination of new genera is restricted to *Timorcranium* in the Wuchiapingian and a reduction in diversity from nine in Wuchiapingian and seven genera in Changhsingian, and then the complete disappearance of the entire group during the Permian-Triassic extinction.

On the one hand, it seems quite obvious that trilobite the diversity declined during the biocrises of the Guadalupian mass extinction events and continued to decline throughout the Lopingian. However, Guadalupian–Lopingian trilobites may exhibit the “Signor-Lipps effect” (Signor and Lipps, 1982), in which the “alleged extinction” of trilobites before the Capitanian in Wordian events, as well as before the EPME events, may be due to sampling bias and incomplete palaeontological records.

It is possible that such a distortion may be due primarily to the fact that the geological sections of the Guadalupian are more widespread than those of the Lopingian. Thus, “The Paleobiology Database (PBDB)” contains information about 453 formations of marine origin of the Cisuralian, 265 of the Guadalupian and 206 of the Lopingian. It is also worth noting that the Guadalupian trilobites have been studied somewhat better and more fully than the Lopingian trilobites. Some works (e.g., Tumanskaya, 1935) show not so much the true diversity of Guadalupian trilobites, but rather the extensive material collected by the author during long and painstaking research. No less significant in understanding the distortion under discussion is the fact that the duration of the Guadalupian is 13.9 Ma, and the Lopingian is half as long – 7.2 Ma (Permophiles, 2023, p. 49), which accordingly can

indicate that the total number of trilobite taxa in Guadalupian (29 genera), other things being equal, should be higher than in Lopingian (nine genera).

Chinese researchers (Shi et al., 2016) reported numerous finds of trilobites *Ditomopyge* (*Carniphillipsia*) cf. *chongqingensis* from the Upper Changhsingian deposits in the Zhongliangshan Section, located in Chongqing, China. Moreover, these remains come from beds of volcanic ash. The authors noted that the number of trilobites decreased in the section with each subsequent bed of volcanic ash. In their opinion, the temporal coincidence between volcanic eruptions and the disappearance of trilobites and other species supports the idea of a cause-and-effect relationship between these events. Trilobites in the ash bed of the Zhongliangshan Section appear before the extinction of the *Clarkina yini* conodonts and the culmination of a negative carbon isotope excursion, which means that the onset of the mass extinction began in Lopingian. Explosive volcanic events caused massive releases of CO₂, toxic gases and volcanic ash and led to habitat loss for some species in Tethys waters. This phenomenon could lead to the sudden death of trilobites and the catastrophic disappearance of the biodiversity of other groups of marine and terrestrial fauna.

However, in this case, what about the trilobites that were recorded in the Lopingian in the mid, close to the high latitudes – in Spitsbergen and New Zealand (Figure 13G)? There is no clear evidence of volcanic activity in these sections. In general, it is difficult and speculative to talk about the unambiguous reason for the disappearance of trilobites at the Permian-Triassic boundary, since there are many different points of view on this matter.

Recently, researchers have questioned whether Permian trilobites could be considered “living fossils” in relation to before-Permian trilobites (Hopkins et al., 2023). In their opinion, the low taxonomic richness, small geographical range, and morphological dullness and other characteristics of

Permian trilobites allow them to be called relicts, although not in all respects.

It is interesting to note that in the terminal part of the Changhsingian Dalong Formation in the Xinmin Section (Anshun, Guizhou, China) trilobite *Pseudophillipsia* cf. *chongqingensis* in carbonaceous mudstone bentonite beds overlain by marl with the conodont *Clarkina meishanensis*, indicating that these trilobites originate from the major extinction event layer (Feng et al., 2011, fig. 3). Trilobites appear to exhibit another interesting effect called “Dead Clades Walking” (Jablonski, 2002). Some relatively small populations of trilobites may have survived the major events of the EPME, and then disappeared after, perhaps even during very the Early Triassic.

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