

The first known fossil hygropetric beetle larva related to *Myxophaga* (Coleoptera) from the Permian of European Russia

Первая находка ископаемой гигропетрической личинки жука, родственной *Myxophaga* (Coleoptera), из перми Европейской России

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КЛЮЧЕВЫЕ СЛОВА: Schizophoromorpha, Torridincolidae, Megaloptera, дыхальцевые жабры, пластронное дыхание, водные насекомые, эволюция, филогения, мезозой.

ABSTRACT. A unique disc-like beetle larva from the Middle Permian (Wordian, ~265 Ma) of Kargala near Orenburg, Cisuralia, *Circularva reichardti* gen. et sp. n., is tentatively assigned to ancestors of Torridincolidae (*Myxophaga*), extinct Phoroschizidae (= Schizophoridae). The filiform gills on its abdomen appear to be of the same type as the plastron-bearing spiracular gills in its living relatives. It is the first fossil hygropetric larva and the earliest fossil evidence of plastron respiration.

РЕЗЮМЕ. Уникальная дисковидная личинка жука из средней перми (уржумский век, ~265 млн. лет) Каргалы близ Оренбурга в Приуралье, *Circularva reichardti* gen. et sp. n., предположительно отнесена к предкам Torridincolidae (*Myxophaga*), вымершим Phoroschizidae (= Schizophoridae). Нитевидные жабры на ее брюшке, по-видимому, того же типа, что и покрытые пластроном дыхальцевые жабры у ее современных родственников. Это первая ископаемая гигропетрическая личинка и древнейшее ископаемое свидетельство пластронного дыхания.

Among numerous Permian insect sites in European Russia, Kargala (or Kargaly) near Orenburg was the first to be discovered, in the 19th century [Nechaev, 1894; Handlirsch, 1904]. Copper sandstones at Kargala were mined from prehistoric times to the early 20th century [Chernykh, 2004], and diverse fossils were collected, the insects mainly from the spoil-heaps of abandoned mines. This non-marine flora and fauna (bivalves, conchostracans, ostracods, insects, fishes, tetrapods) was buried in deltaic deposits [Efremov, 1954]. The rich and diverse insect assemblage contains several groups of amphibiotic

insects [Martynov, 1937], including schizophoromorph beetles, and is dated Guadalupian (Wordian, ~265 Ma; Middle Permian, Urzhumian in the Russian stratigraphic scale) [Shcherbakov, 2008]. Autumn 2013 the field party of Borissiak Paleontological Institute, Russian Academy of Sciences (PIN) collected several hundred insects at Kargala, including a unique minute arthropod of almost perfect disc shape.

This onisciform (i.e. oval, flattened) creature was identified as a holometabolan larva based on three thoracic segments (especially their lateral lobes) somewhat enlarged relative to the following ten abdominal ones, and stemmata instead of compound eyes (see Discussion). Onisciform larvae are known in Coleoptera and some Diptera and Lepidoptera; of these three orders, only the beetles have already existed in the Permian. Long, filiform gills on sides of the abdomen of the fossil larva relate it to the modern Torridincolidae of the suborder *Myxophaga*. However, the abdominal segment X is much more developed than in the larvae of living myxophagans, arguing for relationship to a more primitive group, the extinct Phoroschizidae (=Schizophoridae; see Discussion). A new genus and species are established for this fossil below.

The smallest of the four coleopteran suborders, *Myxophaga*, comprises four extant families of small to minute beetles feeding on algae and distributed worldwide [Crowson, 1955; Beutel, Leschen, 2005]. These families are classified into two superfamilies, Lepicerioidea (Lepiceridae) and Sphaeriuoidea: Torridincolidae (including Deleveinae), Hydroscahidae, Sphaeriusidae (= Sphaeriidae = Microsporidae) [Ge et al., 2010; Bouchard et al., 2011; Kirejtshuk, Poinar, 2013; Jałoszyński et al., 2017]. Torridincolidae occur in hygropetric habitats (on

rock surfaces covered with a thin film of moving water or located in the spray zone beneath waterfalls), sometimes in temporary streams, Sphaeriusidae in wet sand or gravel at the edges of streams or rivers, and Hydrosaphidae on algae over which a thin film of water is flowing or under rocks in streams; larvae of most torridincolid genera are flattened dorsoventrally, and larvae of two other families only slightly so [Lawrence, Reichardt, 1991]. Lepiceridae occur along streams, and their larvae are still unknown [Lawrence et al., 2019].

Four species of Lepiceridae and four species of Sphaeriusidae, some of them assigned to extant genera, are recorded in mid-Cretaceous Burmese amber (earliest Cenomanian, ~99 Ma) [Kirejtshuk, Poinar, 2006, 2013; Kirejtshuk, 2009; Jałoszyński et al., 2017, 2020; Fikáček et al., 2023; Li et al., 2023]. Five fossil species of Hydrosaphidae are known. *Hydrosapha? jeholensis* Cai, Short et Huang, 2012 is described from the Early Cretaceous Yixian Formation (early Barremian, ~125 Ma) of China [Cai et al., 2012]. Two myxophagan species were recorded from the Triassic: *Leehermania prorova* Chatzimanolis, Grimaldi et Engel, 2012 from the Cow Branch Formation (early Norian, ~226 Ma [Fraser et al., 2017]) of Virginia, described as a staphylinid and reinterpreted as a myxophagan closest to Hydrosaphidae [Fikáček et al., 2020], and *Triamyxa coprolithica* Qvarnström et al., 2021 found in dinosauriform coprolites from Krasiejów (late Carnian, 232–227 Ma) of Poland, placed in a monotypic family similar to Hydrosaphidae [Qvarnström et al., 2021]. Kirejtshuk et al. [2023] included these two Triassic taxa to Hydrosaphidae as subfamilies Leehermaniinae and Triamyxinae, and added to the latter subfamily *Palaeosapha tunguskaensis* Kirejtshuk, Prokin et Ponomarenko, 2023 from the Permian-Triassic boundary beds (~252 Ma) of the Tunguska Basin. Yet another Triassic myxophagan from Tongchuan, China (late Ladinian, 238–237 Ma) [Zheng et al., 2018, fig. 3L] apparently belongs to Hydrosaphidae as well (A.G. Kirejtshuk, pers. comm.). Torridincolidae have not been recorded as fossils.

The larvae of Sphaeriusoidea have a very peculiar respiratory system, spiracular gills (gills associated with spiracular openings) [Hinton, 1967]. Gills of this type are also reported in the larvae of some Elmidae [Spangler, 1990], but otherwise confined to the pupal stage and found in Torridincolidae, Psephenidae, and various Diptera. Spiracular gills bear a plastron (permanent gas gill held in place by hydrofuge cuticular modifications), except for those in pupae of *Chironomus* and allied genera [Hinton, 1968: 161]. Spiracular gills functioning as well in air as in water are adaptations to life in the splash zone of streams or biotopes subject to fluctuating water levels [Lancaster, Downes, 2013]. In the larvae of Torridincolidae spiracular gills are long, slender, 2–3-segmented, with subterminal spiracular opening, proximally annulate, covered with plastron mesh, and inserted laterally or laterodorsally on abdominal tergites I to VIII [Reichardt, 1973; Vanin, Costa, 2001]. In other Sphaeriusoidea spiracular gills are short, balloon-like or tufted, with terminal spiracular opening, and set on abdominal tergites I to VIII (Sphaeriusidae) or on pronotum and tergites I and VIII (Hydrosaphidae) [Beutel et al., 1999]. Torridincolidae and Hydrosaphidae

are the only known insects in which plastron respiration evolved in the three life stages—larvae, pupae and adults (at least in some species). Torridincolids have been named the “most aquatic” of all water beetle families [Jäch, 1998], but they are very special, hygropetric water beetles.

A diverse and abundant group of fossil schizophoromorph beetles (Middle Permian–Cretaceous), considered to be ancestral to the Myxophaga, contains the families Schizophoridae and Catiniidae (= Coleocatiniidae; both Schizophoroidea), Rhombocoleidae and Asiocoleidae (= Tricoleidae), and the form family Schizocoleidae [Ponomarenko, 1969, 2011]. Bouchard and Bousquet [2020] replaced the family name Schizophoridae based on a junior homonym with Phoroschizidae, and derived the superfamily name from Schizocoleidae, but the latter is not suitable for this purpose, since it is a form family for isolated elytra of a certain type, not necessarily belonging to schizophoroid beetles (see Discussion). Living myxophagans represent isolated relicts of an early schizophoroid radiation [Lawrence, Newton, 1982]. Ponomarenko [1973, 2002] united schizophoroids, rhombocoleids and asiocoleids with Micromalthidae and extant myxophagan families (as Microsporoida) into the infraorder Schizophoromorpha of the ancestral suborder Archostemata s.l. Conversely, Bouchard et al. [2011] assigned the extinct schizophoromorph families to the suborder Myxophaga in the broad sense.

The type material of the new taxon is deposited at the Borissiak Paleontological Institute (PIN). The fossil was photographed using a Leica MZ9.5 stereomicroscope, Zeiss Axioplan 2 microscope, and Leica DFC420 camera, and imaged without coating with backscattered electron (BSE), secondary electron (SE) and low vacuum secondary Tescan (LVSTD) detectors of Tescan Vega2 and Vega3 XMU scanning electron microscopes.

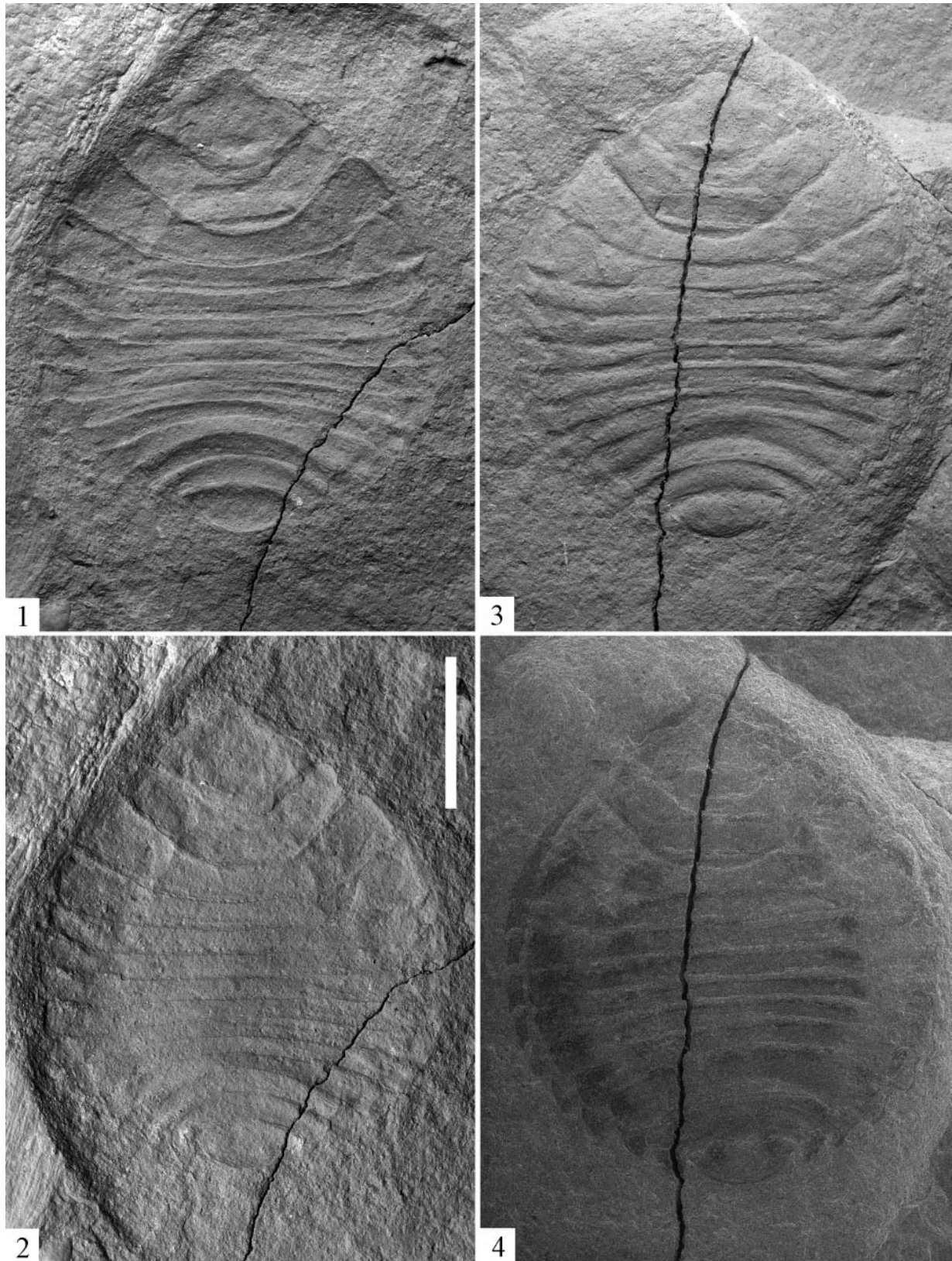
Suborder Archostemata Kolbe, 1908

Infraorder Schizophoromorpha Ponomarenko, 2002
Family ?Phoroschizidae Bouchard et Bousquet, 2020
(= Schizophoridae Ponomarenko, 1968)

Circularva Shcherbakov et Ponomarenko, **gen.n.**

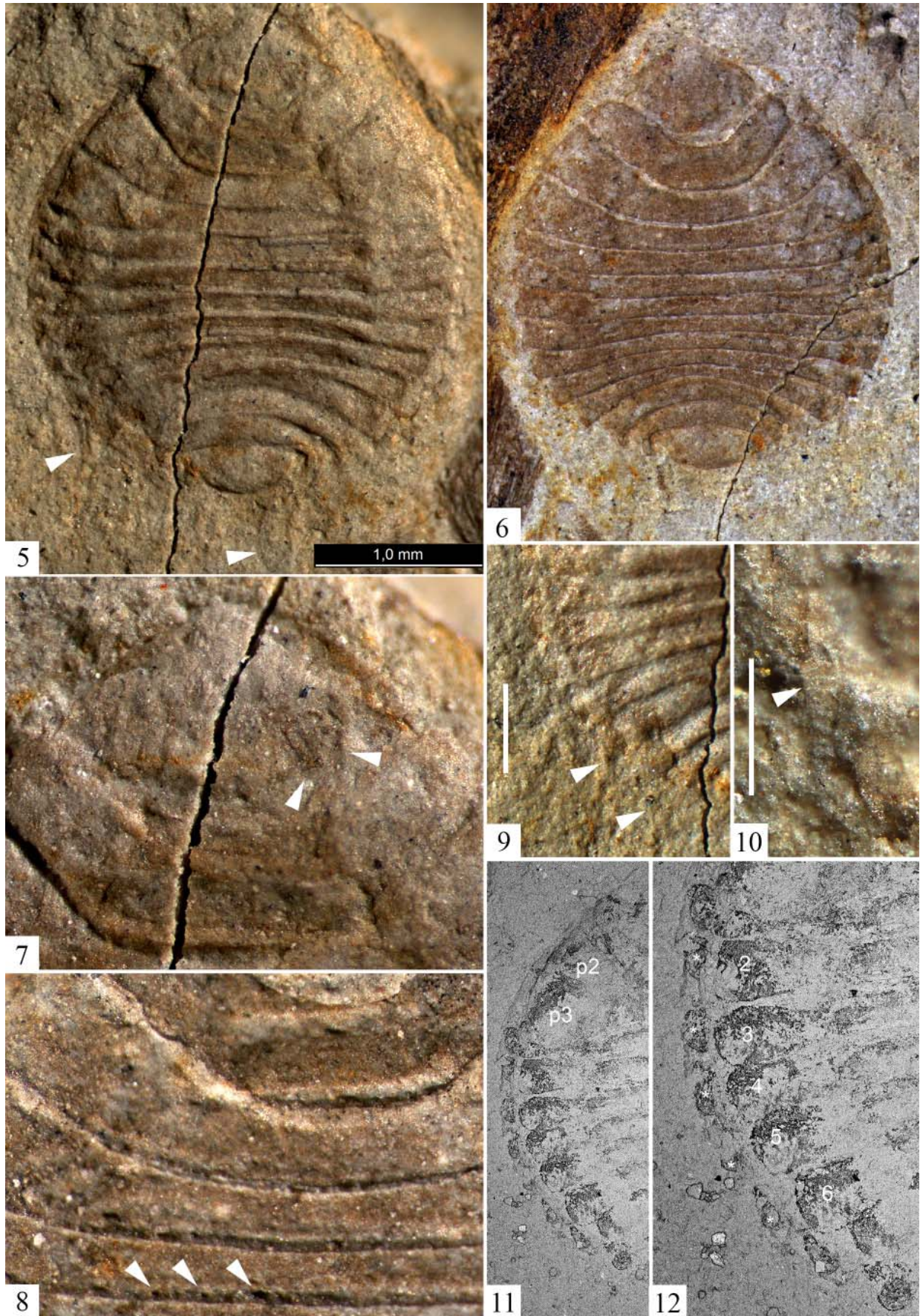
TYPE SPECIES. *Circularva reichardti* Shcherbakov et Ponomarenko, **sp.n.**

DIAGNOSIS. Small, flattened larva resembling sucking disc. Body contour almost perfectly circular, except for head angularly projecting anteriorly. Thoracic and abdominal tergites with lateral lobes (paranota, or paratergites, or dorsal laterotergites) feebly separated by depressed lines from disc; paranota widest at mesonotum, narrower and less distinctly separated towards posterior; disc widest at abdominal segment III. Head large, transverse, nearly diamond-shaped in dorsal view, longer than pronotum, jutting into body, so that pronotum U-shaped and mesonotum deeply arched. Stemmata on each side six, in sublateral group, facing dorsally. Thorax ~1.5 times shorter than abdomen. Meso- and metanotum and at least anterior abdominal tergites with posterior row of widely separated setigerous tubercles. Abdominal paranota of successive segments contiguous, not festoon-like. Posterolateral angles of abdominal tergites acute, in posterior tergites (especially IX) produced tooth-like. Long, filiform spiracular gills finely annulate proximally, originating sublaterally, directed caudally, ap-



Figs 1–4. *Circularva reichardtii* gen. et sp.n., habitus: 1–2 — negative, 3–4 — positive impression. SEM: 1–3 — BSE, 4 — LVSTD. Scale bar 1 mm.

Рис. 1–4. *Circularva reichardtii* gen. et sp.n., общий вид: 1–2 — обратный, 3–4 — прямой отпечаток. СЭМ: 1–3 — BSE, 4 — LVSTD. Длина масштабной линейки 1 мм.



parently developed on all tergites from I to IX. Tergite X large, almost semicircular, completely visible from above.

COMPOSITION. Type species.

COMPARISON. The presence of long spiracular gills on the abdomen indicates that the fossil belongs to either Torridincolidae or their ancestors, Phoroschizidae (= Schizophoridae; see Discussion). The new genus differs from presumed larvae of Schizophoromorpha in the disc-shaped body, from known torridincolid larvae in the large abdominal segment X, from Torridincolinae in the shorter thorax, and from Deleveinae in contiguous abdominal paranota.

The long spiracular gills and the disc-shaped body of the new genus, flattened like in torridincolids, suggest life in running water. The degree of larval body flattening is variable in Torridincolidae, being greatest in the last instar larvae of advanced genera [Reichardt, 1973; Ge et al., 2010], so the new fossil is presumably a mature larva.

ETYMOLOGY. Latin *circus* (ring) and *larva* (ghost, mask); gender feminine.

Circularva reichardti Shcherbakov et Ponomarenko,

sp.n.

Figs 1–13.

MATERIAL. Holotype PIN 199/379 (part and counterpart), mature larva; spoil-heaps of Kuzminovskii Mine 65 km NNW Orenburg, abandoned Kargala [Kargaly] copper mines, Orenburg Province, SE European Russia; Guadalupian (Middle Permian), Wordian (Urzhumian), Bolshaya Kinel Formation, *Estemmenosuchus uralensis* tetrapod zone [Golubev, 2000; Sennikov, Golubev, 2017].

DESCRIPTION. Body 3.3 mm long, 3.0 mm wide. Dorsum moderately convex at life, flattened at burial (flat medially and sloping at sides; tergites VII–IX retaining original arched shape but tilted towards bedding plane; preceding tergites flattened, slightly telescoped medially and drawn apart laterally; dorsal head surface less sloped than at life). Head transverse (1:1.7), slightly convex in central part, with a pair of shallow depressions at anterior margin, lateral angles acute. Antennae not visible. Thoracic segments rather short along midline (pronotum 0.7 as long as meso- + metanotum there); meso- and metathoracic paranota much longer at lateral margin than at base, whereas prothoracic and segment I paranota slightly shorter at lateral margin than at base. Setigerous tubercles along hind margin of thoracic and abdominal tergites preserved as pits on counterpart. Thoracic and abdominal sternites wide (~1/2 and 2/3 segment width, respectively), their posterior margins straight. Leg bases indicated by depressions at sides of thoracic sternites; legs not visible, apparently short. Abdominal segments with small rounded epipleurites (clearly visible on left side, distorted and curved on right side) and much wider hypopleurites. Spiracular gills originating sublaterally from emarginations developed near posterolateral angles

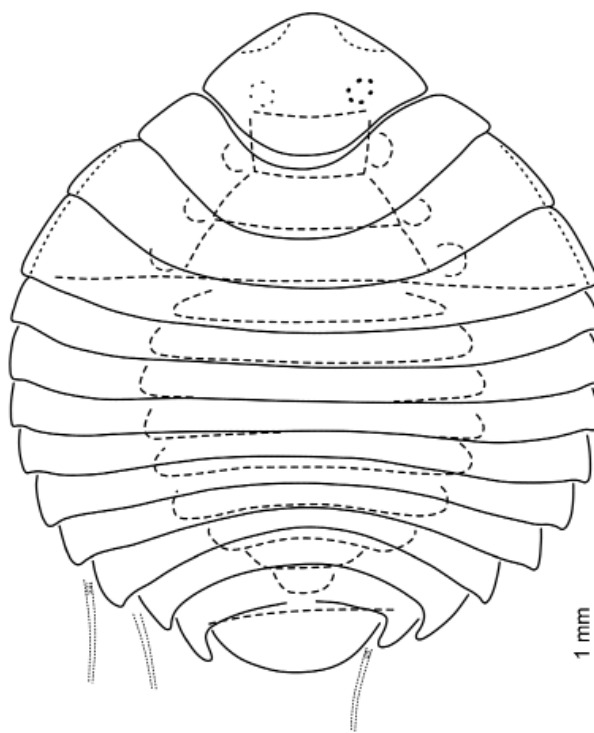


Fig. 13. *Circularva reichardti* gen. et sp.n., dorsal habitus; structures of ventral side in dashed line.

Рис. 13. *Circularva reichardti* gen. et sp.n., общий вид сверху; структуры вентральной стороны пунктиром.

of tergites I–IX; gills visible on some posterior abdominal segments (those of anterior segments possibly superimposed onto abdomen; gill visible caudad of segment X belongs to segment IX); gills no less than 0.5 mm long, annulate proximally, smoothly curved (probably not segmented); plastron mesh and spiracular openings not visible. Tergite X as wide as head, 2.5 times as wide as long, medially not separated from tergite IX. Body somewhat darkened; gills pale.

ETYMOLOGY. After Hans Reichardt, Brazilian entomologist, an expert on Myxophaga.

Discussion

Schizophoroids and Torridincolidae. Phoroschizidae (=Schizophoridae), Catiniidae, Asiocolidae, and Rhombocoleidae possess so-called schiza, the ridge or tongue on the underside of the elytron interlocking with the body, interpreted

Figs 5–12. *Circularva reichardti* gen. et sp.n.: 5–6 — habitus (arrows, spiracular gills); 7 — head (on crosshair of arrows, centre of group of stemmata); 8 — meso- and metanotum and anterior abdominal tergites (arrows, setigerous tubercles); 9 — left side of abdomen (arrows, spiracular gills of segments VI and VII); 10 — base of spiracular gill of segment VI (annulations visible); 11 — left side, meso- (p2) and metapleuron (p3); 12 — same, enlarged, abdominal epipleurites (asterisks) and hypopleurites (numbered). Positive (5, 7, 9–12) and negative impression (6, 8). Polarized light (6); SEM (BSE: 11, 12). Scale bar: 1 mm (5), 0.5 mm (9), 0.2 mm (10).

Рис. 5–12. *Circularva reichardti* gen. et sp.n.: 5–6 — общий вид (стрелки — дыхальцевые жабры); 7 — голова (на перекрестье стрелок центр группы стемм); 8 — средне- и заднеспинка и первые тергиты брюшка (стрелки — щетинконосные бугорки); 9 — левая сторона брюшка (стрелки — дыхальцевые жабры сегментов VI и VII); 10 — основание дыхальцевой жабры сегмента VI (видна кольчатость); 11 — левая сторона, мезо- (p2) и метаплеврит (p3); 12 — то же, увеличено, брюшные эпиплевриты (звездочки) и гипоплевриты (пронумерованы). Прямой (5, 7, 9–12) и обратный отпечаток (6, 8). Поляризованный свет (6); СЭМ (BSE: 11, 12). Длина масштабной линейки: 1 мм (5), 0.5 мм (9), 0.2 мм (10).

as an adaptation for storing the air under the elytra, and evidence of aquatic lifestyle, despite the absence of swimming adaptations in these families [Ponomarenko, 1968, 2003b, 2011, 2013]. Such an interlocking tongue (sometimes situated more caudally) is also found in Triaplidae (end-Permian to Triassic Haliploidea), Timarchopsinae (=Necronectinae, Mesozoic Coptoclavidae, Dytiscoidea), and many other extant beetle families of three suborders: Myxophaga (except Hydrosaphidae), Adephaga (Haliploidea, Meruidae, Aspidytidae, Noteridae, Hygrobiidae, Amphizoidae, some Dytiscidae, some Carabidae), and Polyphaga (some Hydrophiloidea, some Scirtioidea, some Byrrhoidea (including Dryopoidea), some Buprestoidea, some Curculionoidea, etc.) [Ponomarenko, 1968, 1977; Lawrence et al., 2011; Lawrence, Ślipiński, 2013]. Isolated smooth elytra with schiza may belong to any suborder, so genera based on such fossils are referred to the form family Schizocoleidae [Ponomarenko, 1968, 2011].

Among Myxophaga, Torridincolidae are most diverse morphologically and taxonomically and approach extinct schizophorids most closely [Lawrence, Reichardt, 1991]. Phoroschizidae (=Schizophoridae; Middle Permian–Cretaceous) are similar to Torridincolidae in many adult characters: head often prognathous and retracted into prothorax, 11-segmented antennae without club, elytra with interlocking tongue, hindwing with oblongum, 5-segmented tarsi, five abdominal ventrites, prosternal process well-developed (often broad, apically convex, in contact with mesoventrite), and metanepisternum participating in bordering mesocoxal cavities (archostematan feature retained also in some Adephaga and Polyphaga) [Lawrence et al., 2011]. The elytra of Deleveinae [Bilton, Mlambo, 2023] and Phoroschizidae lack serial punctures, while the elytra of Torridincolinae with 9–13 striae [Perkins, Bergsten, 2019] more closely resemble those of Rhombocoleidae and Asiocolidae (indicating that the superfamily rank given to these fossil groups could be exaggerated). Torridincolidae are more derived than Phoroschizidae in the very short antennae with modified scape and pedicel, very broad prosternal process, meta-ventrite without transverse suture, proximal tarsomeres very short, and abdominal ventrites II–IV short. Torridincolids are 1.0–2.9 mm long, whereas described schizophorids are larger, at least 5 mm long. However, there are Permian schizocoleid elytra of minute size, e.g. Late Permian *Pseudochrysomelites ovum* 1.5–1.8 mm long [Ponomarenko, 2004, 2013] belonging to the beetles 2.0–2.4 mm long, almost surely Phoroschizidae (only a few finds of the earliest Adephaga and Polyphaga are known from the Permian, see below). Even smaller schizocoleid elytra up to 0.82 mm long (corresponding to beetles about 1.1 mm long) are found in the Permian–Triassic boundary beds [Ponomarenko, 2015]. On the other hand, Catiniidae (Triassic–Cretaceous) are similar rather to Hydrosaphidae in the prosternal process very short and pointed.

Affinities of *Circularva* gen.n. Body shapes reminiscent of *Oniscus* isopods have evolved many times in various arthropod groups, including crustaceans, millipedes, and insects. All Isopoda like other Malacostraca have their trunk clearly divided into a large thorax containing at least six free large segments, and a shorter and narrower abdomen, consisting of no more than five smaller segments [Schram, 1986]. In onisciform Diplopoda, trunk tergite II is often enlarged, more rarely either only tergite III or both tergites III and IV, while tergite I (collum) is usually relatively small [Golovatch, 2003]. On the contrary, *Circularva* gen.n. shows insect tagmosis: a three-segmented thorax, clearly differentiated from a ten-segmented abdomen, with thoracic tergites longer than the abdominal tergites (though only moderately, as e.g. in larvae of *Delevea* Reichardt, 1976, non-torridincolid Myxophaga, Amphizoidae, and many other beetles). The insect nature of *Circularva* gen.n. is confirmed by its wide, well sclerotized thoracic and abdominal sternites

separated by straight intersegmental boundaries, and the leg bases at the sides of thoracic sternites. In millipedes, the sternites are small and the leg bases are close to the mid-ventral line, while in isopods, the sternal sclerotizations are less developed, paired, with curved boundaries, and the legs have the first free segment long, attached laterally and directed medially.

Somewhat enlarged lateral lobes (paranota) of meso- and metanotum indicate that *Circularva* gen.n. is a pterygote immature (or wingless adult). These lobes, which do not protrude caudad to form wingpads, and the stemmata instead of compound eyes, allow to distinguish the fossil from onisciform nymphs of Palaeodictyoptera, Blattodea, and Hemiptera. Moreover, the new fossil is distinct from Blattodea in the shape of pronotum, and from Hemiptera in the abdominal tergites VIII–IX not deeply U-shaped, segment X large, and anal opening not dorsal. Therefore, this fossil is a holometabolan larva.

Among Holometabola, onisciform, sometimes disc-like larvae are met with in various groups of Coleoptera, as well as in some advanced families of two orders not known from the Permian — Diptera (e.g. Platypezidae) and Lepidoptera (e.g. Lycaenidae). Two characters of the ventral side confirm that *Circularva* gen.n. is a beetle larva. (a) Two rows of sclerites in the lateroventral area of the abdomen, epipleurites and hypopleurites, looking like e.g. in Carabidae and resembling the embryonal configuration [Kobayashi et al., 2013]. (b) The thoracic metapleura are slightly longer than the mesopleura (as e.g. in Torridincolinae [Perkins, Bergsten, 2019] and Elmidae [Shepard, 2020]); beetles are the only posteromotoric holometabolans.

Onisciform beetle larvae are known in Myxophaga (Torridincolidae), Adephaga (Amphizoidae, Cychrimi), and various groups of Polyphaga (Silphidae, Scydmaeninae, Scirtidae, Byrrhidae, Elmidae, Psephenidae, Brachypsectridae, Lampyridae, Cerylonidae, Discolomatidae, Endomychidae, Coccinellidae, Corylophidae, Tenebrionidae, Chrysomelidae). In *Circularva* gen.n. the head is large, entirely visible from above, longer than the pronotum, like in some Torridincolidae (e.g. *Delevea* [Endrödy-Younga, 1997, pl. 7B]), Amphizoidae, and Brachypsectridae, whereas in onisciform larvae of the other Polyphaga the head, sometimes small and retractable, is more or less concealed by (or at least shorter than) the pronotum in dorsal view. The fossil shows neither urogomphi nor branched lateral processes and spine-like terminal segment, in contrast to amphizoid or brachypsectrid larvae. Instead, it possesses filiform sublateral abdominal gills, like in Torridincolidae. Such detail as proximal gill annulations allow to assume that these fossil gills were designed like in living torridincolids, i.e. with spiracular openings and plastron mesh, although neither of the last two characters is visible.

Several other features shared by *Circularva* gen.n. and some Torridincolidae genera support the assumption of its relationship with this family. In the large diamond-shaped head, contiguous abdominal paranota, and dorsolateral position of spiracular gills, the new genus is most similar to *Torridincola* Steffan, 1964 [Steffan, 1964, fig. 9], but in the latter the anterior pronotal margin is only slightly sinuate, and the segment X is transformed into paired anal flaps scarcely visible from above. In the short thorax and setigerous tubercles on tergites, the fossil is similar to *Delevea*, but in the latter the body is elongate, and the pronotum is longer than mesonotum. The legs of the fossil were apparently short, not visible from above, like in *Satonius* Endrödy-Younga, 1997 and *Ytu* Reichardt, 1973, but in these latter abdominal paranota of successive segments are widely separated, festoon-like, bearing spiracular gills on their apices.

However, still other features of *Circularva* gen.n. are more primitive than in all known larvae of Myxophaga.

(1) Stemmata on each side 6, vs. 5 in Hydroscaphidae, 4 in Sphaeriusidae, 4 or 3 in Torridincolidae [Beutel et al., 1999; Vanin, Costa, 2001]. Six is the primitive number of stemmata, found in most families of Adephaga and several groups of Polyphaga, including most Hydrophilidae. The fossil is peculiar in the dorsolateral position of stemmata, in contrast to lateral in Myxophaga; the area of stemmata is flat (on a distinct elevation in Torridincolidae).

(2) The abdominal segment X is large, not concealed by the segment IX, whereas myxophagans have the segment X diminished, rarely visible from above (see e.g. [Böving, Craighead, 1931, pl. 9]), sometimes split into 2–3 lobes. The well-developed segment X is presumably an ancestral condition in the larvae of Coleoptera [Lawrence, Ślipiński, 2013]. This difference could be considered very important if it were not for the coexistence of both states of the larval segment X (well developed or reduced) within certain families. Both of these states are found not only in such a large and diverse family as Hydrophilidae [Archangelsky, 1998], but even in such a small and homogeneous family as Haliplidae—segment X reduced in *Peltodytes* Régimbart, 1879, singled out into the subfamily Peltodytinae [Böving, Craighead, 1931], but large and visible from above in other genera [Lawrence, Ślipiński, 2013; Makarov, Prokin, 2015]. The semicircular shape of the segment X is unknown in other beetle larvae.

(3) Nine pairs of spiracular gills, vs. eight in Torridincolidae. The number of abdominal segments bearing tracheal gills varies within Haliplidae (8 or 9) and Hydrophilidae (7 or 8).

(4) Two rows of sclerites in the lateroventral area of the abdomen, a primitive condition, not recorded in Myxophaga.

Megalopteran-like beetle larvae. From the same Permian fossil site as *Circularva* **gen.n.**, one more aquatic larva was reported. This large (24 mm long), elongate larva with 10-segmented abdomen bearing tracheal gills on the segments I–IX was originally assigned to Megaloptera and to the genus *Permosialis* Martynov, 1928 [Sharov, 1953], but later this genus, based on adults, was transferred to Miomoptera, believed to be terrestrial insects [Riek, 1976], and the larva was re-interpreted as that of Coleoptera, namely Gyrinidae [Beutel, Roughley, 1988]. Various similar larvae from the Middle Triassic Voltzia Sandstone, Vosges (Early Anisian, ~245 Ma) were attributed to Megaloptera [Marchal-Papier, 1998]. Later, all these larvae were assigned to the coleopteran infraorder Schizophoromorpha, the above-mentioned larva from Kargala was redescribed, named as *Kargalarva permosialis* Prokin, Ponomarenko et Kirejtshuk, 2019 and tentatively associated with Rhombocoleidae [Prokin et al., 2013, 2015, 2019], and another larva of this type was described from the Late Triassic of Germany [Prokin, Bashkuev, 2021]. Among living beetles, megalopteran-like larvae (i.e. elongate with paired tracheal gills on abdominal segments) are known in the most primitive Adephaga (Gyrinidae, some Haliplidae and Dytiscidae) and some primitive Polyphaga (some Hydrophilidae, e.g. *Hydrochara* Berthold, 1827, *Berosus* Leach, 1817).

At first glance the onisciform larvae of Torridincolidae and *Circularva* **gen.n.** look very dissimilar to the megalopteran-like larvae of primitive hydradephagans, some hydrophilids, and presumably also schizophoromorphs. However, the gap is partly bridged by the larvae of the most primitive torridincolid genus *Delevea* and the early instar larvae of derived torridincolids [Reichardt, 1973; Beutel et al., 1999]—more elongated, less flattened, with proportionally greater, leg-like tracheal (spiracular) gills on the abdomen, and thus more megalopteran-like. Moreover, *Kargalarva* and *Circularva* **gen.n.** share with the larvae of Gyrinidae and some Haliplidae two important primitive characters: well-developed abdominal segment X visible from above, and abdomen with 9 pairs of tracheal gills. Therefore, the

find of *Circularva* **gen.n.** agrees with supposition that Schizophoromorpha, the earliest Adephaga [Ponomarenko, 1977; Erwin, 1979], and possibly also the earliest Polyphaga were aquatic or riparian [Ponomarenko, 1983] and had megalopteran-like larvae.

Placing the new genus into the system of Coleoptera. The long, sublateral, proximally annulate spiracular gills developed on the abdominal segments is a derived character shared by the new genus only with Torridincolidae. The features shared by *Circularva* **gen.n.** with one or another torridincolid genus (disc-like body, diamond-shaped head, short legs, contiguous abdominal paranota, setigerous tubercles on tergites) also support this relationship, but can only be regarded as shared traits. However, the other characters (six stemmata in laterodorsal position, large segment X, nine pairs of spiracular gills) demonstrate that the fossil is more primitive than all known torridincolids.

If we consider larval spiracular gills of specific structure as a unique synapomorphy of Torridincolidae, then we can assign *Circularva* **gen.n.** to this family. The differences in the number of stemmata and gills and degree of segment X development do not contradict this placement, so far as these three characters are variable within such a polymorphic family as Hydrophilidae, and two latter in Haliplidae as well. If so, then the present-day torridincolids are relics of a more diverse family that left nearly no trace in the fossil record due to taphonomically unfavourable mode of life.

However, tracheal gills could have evolved into spiracular gills of the torridincolid type already in some schizophoroids, and be inherited by torridincolids, while modified or lost in remaining Myxophaga. Then torridincolid-type spiracular gills represent a synapomorphy of all myxophagan families, subsequently lost in all of them but torridincolids. If so, similarities of the new genus to *Kargalarva* in retaining 9 pairs of tracheal gills and the well-developed segment X may be interpreted as evidence to assign *Circularva* **gen.n.** to a group more primitive than Torridincolidae.

In the case, the new genus probably belongs to Phoroschizidae (or some other, possibly unknown, extinct group). Schizophoromorphs, including the small ones, are quite common in the fossil assemblage of Kargala. The estimated length 2.0–2.4 mm of the Late Permian beetle *Pseudochrysolites ovum* (Ponomarenko, 2004), described in Schizocoleidae based on five isolated elytra [Ponomarenko, 2004, 2008], corresponds well to the 3 mm long *Circularva* larva (the adults are somewhat smaller than the mature larvae in torridincolids). These smallest schizophoroids (up to now known only from isolated elytra) were even smaller than the largest Torridincolidae (2.9 mm).

Regardless of which of these two families the new genus is placed in, it deserves separation at the subfamily level due to important differences from both torridincolid and putative fossil schizophoromorph larvae. Among fossil aquatic beetles, three families were based on larvae: Coptoclavidae, Parahygrobiidae, and Colymbotethidae, all Dytiscoidea [Ponomarenko, 1977, 1994]. However, classification of Coleoptera relies generally on adult characters. Therefore, we consider establishing a subfamily for *Circularva* **gen.n.** to be premature and tentatively assign it to Phoroschizidae (=Schizophoridae).

There is little chance for the *Circularva* adult to be found and recognized among beetle fossils. For living insects, larvae may be associated with adults on direct (rearing, DNA sequences) or indirect (common occurrence) evidence. For compression fossils, only the latter is applicable, and only for rather common taxa of limnic (amphibiotic and aquatic) insects spending (most of) their nymphal/larval and adult life in/near the water bodies producing fossiliferous sediments. In compression fossil assemblages dominated by limnic insects, rheophiles are very rare—only one specimen of *C. reichardti* **sp.n.** from about one thousand total

insects collected at Kargala, so the chance of finding another such larva or conspecific adult is very small. Adult Torridincolidae are not as distinctive as their larvae in characters usually preserved in compression fossils, so even if found, a *Circularva* adult may pass unnoticed among Phoroschizidae or (if represented with an isolated elytron) Schizocolleidae.

Plastron respiration. Whether *Circularva* **gen.n.** belongs to Torridincolidae or their ancestors, one may conclude that by the Middle Permian the beetles of schizophoroid lineage (Schizophoromorpha = Myxophaga s.l.) already had diverse aquatic larvae, not only resembling those of Megaloptera and Gyrinidae, but also highly specialized rheophilic plastron-bearers, adapted for life in hygropetric habitats.

Plastrons are widespread in insects, arachnids, and even in plants subject to drowning in their wetland habitats [Thorpe, 1950; Heckman, 1983; Pedersen, Colmer, 2012]. Insect plastrons were in existence in the Mesozoic, at least in those extant families that now possess plastrons among aquatic Heteroptera, Coleoptera, and pupae of Diptera [Brown, 1987; Crosskey, 1991; Hasiotis, 2000; Lukashovich, 2012; Criscione, Grimaldi, 2017]. A covering of modified microtrichia for trapping an air film is found on the underside of elytra in frog-hopper-like Dymorphoptilidae from the Permian-Triassic boundary beds [Shcherbakov, 2022]. The spiracular gills of *Circularva* **gen.n.** are even earlier fossil plastron evidence, though indirect.

On the age of coleopteran suborders. Until recently, the suborders Adephaga, Polyphaga and Myxophaga had no reliable pre-Triassic records, though it was suggested that some isolated elytra of advanced structure from the Late Permian could belong to archaic polyphagan and adephagan taxa [Ponomarenko, 2002]. Now the earliest finds of adult Myxophaga [Kirejtshuk et al., 2023] and Adephaga (Triplidae, rather than Gyrinidae [Volkov, 2013; Kirejtshuk, Prokin, 2018; Yan et al., 2018; Ponomarenko, 2021], Haliplidae [Ponomarenko, Prokin, 2015], and Trachypachidae [Ponomarenko, Volkov, 2013]) are described from the so-called Permian-Triassic boundary beds (Babiy Kamen of the Kuznetsk Basin; Anakit and Untuun of the Tunguska Basin), dated basal Triassic or rather end-Permian [Shcherbakov et al., 2021; Shcherbakov, 2022]. Beetles possibly belonging to Polyphaga are now recorded ~10 Ma earlier than the Permian/Triassic boundary, in the Middle Permian (late Capitanian, ~261 Ma) of China [Yan, Strelnikova, 2022], while elytra characteristic only of Polyphaga are found in the latest Permian (Changhsingian, ~253 Ma) of European Russia [Ponomarenko, 2003a]. The discovery of an even older torridincolid-type larva from European Russia may indicate that Myxophaga also appeared in the Permian.

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References

- Archangelsky M. 1998. Phylogeny of Hydrophiloidea using characters from adult and preimaginal stages // Syst. Entomol. Vol.23. P.9–24. <https://doi.org/10.1046/j.1365-3113.1998.00039.x>
- Beutel R.G., Leschen R.A.B. 2005. Handbuch der Zoologie. Coleoptera, Beetles. Vol.1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim). Berlin: Walter de Gruyter. 567 p.
- Beutel R.G., Roughley R.E. 1988. On the systematic position of the family Gyrinidae (Coleoptera: Adephaga) // Zool. Syst. Evol.-Forsch. Vol.26. P.380–400. <https://doi.org/10.1111/j.1439-0469.1988.tb00324.x>
- Beutel R.G., Maddison D.R., Haas A. 1999. Phylogenetic analysis of Myxophaga (Coleoptera) using larval characters // Syst. Entomol. Vol.24. P.171–192. <https://doi.org/10.1046/j.1365-3113.1999.00075.x>
- Bilton, D.T., Mlambo M.C. 2023. A revision of *Delevea* Reichardt, 1976: a Southern African endemic water beetle genus including the largest known extant myxophagans (Coleoptera: Myxophaga: Torridincolidae) // Zootaxa. Vol.5285. P.311–324. <https://doi.org/10.11646/ZOOTAXA.5285.2.5>
- Bouchard P., Bousquet Y. 2020. Additions and corrections to “Family-group names in Coleoptera (Insecta)” // ZooKeys. Vol.922. P.65–139. <https://doi.org/10.3897/zookeys.922.46367>
- Bouchard P., Bousquet Y., Davies A.E., Alonso-Zaragoza M.A., Lawrence J.F., Lyal C.H.C., Newton A.F., Reid C.A.M., Schmitt M., Ślipiński S.A., Smith A.B.T. 2011. Family-group names in Coleoptera (Insecta) // ZooKeys. Vol.88. P.1–972. <https://doi.org/10.3897/zookeys.88.807>
- Böving A.G., Craighead F.C. 1931. An illustrated synopsis of the principal larval forms of the order Coleoptera // Entomol. Am. (N.S.). Vol.11. P.1–351.
- Brown H.P. 1987. Biology of riffle beetles // Annu. Rev. Entomol. Vol.32. P.253–273. <https://doi.org/10.1146/annurev.en.32.010187.001345>
- Cai C., Short A.E.Z., Huang D. 2012. The first skiff beetle (Coleoptera: Myxophaga: Hydroscaphidae) from Early Cretaceous Jehol biota // J. Paleontol. Vol.86. P.116–119. <https://doi.org/10.1666/11-050.1>
- Chernykh E.N. 2004. Kargaly: The largest and most ancient metallurgical complex on the border of Europe and Asia // Linduff K.M. (ed.). Metallurgy in Ancient Eastern Eurasia from the Urals to the Yellow River. Lewiston: Edwin Mellen Press. P.223–238.
- Criscione J., Grimaldi D. 2017. The oldest predaceous water bugs (Insecta, Heteroptera, Belostomatidae), with implications for paleolimnology of the Triassic Cow Branch Formation // J. Paleontol. Vol. 91. P.1166–1177. <https://doi.org/10.1017/jpa.2017.48>
- Crosskey R.C. 1991. The fossil pupa *Simulimima* and the evidence it provides for the Jurassic origin of the Simuliidae (Diptera) // Syst. Entomol. Vol.16. P.401–406. <https://doi.org/10.1111/j.1365-3113.1991.tb00675.x>
- Crowson R.A. 1955. The Natural Classification of the Families of Coleoptera. London: Nathaniel Lloyd. 187 p.
- Efremov I.A. 1954. [The fauna of terrestrial vertebrates in the Permian copper sandstones of western Cis-Urals] // Tr. Paleontol. Inst. AN SSSR. Vol.54. P.1–416 [in Russian].
- Endrödy-Younga S. 1997. Active extraction of water-dissolved oxygen and descriptions of new taxa of Torridincolidae (Coleoptera: Myxophaga) // Ann. Transvaal Mus. Vol.36. P.313–332. https://hdl.handle.net/10520/AJA00411752_82
- Erwin T.L. 1979. Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions // Erwin T.L., Ball G.E., Whitehead D.R., Halpern A.L. (eds). Carabid Beetles: Their Evolution, Natural History, and Classification. Hague: W. Junk. P.539–592.
- Fikáček M., Beutel R.G., Cai C., Lawrence J.F., Newton A.F., Solodovnikov A., Ślipiński A., Thayer M.K., Yamamoto S. 2020. Reliable placement of beetle fossils via phylogenetic analyses—Triassic *Leehermania* as a case study (Staphylinidae or Myxophaga?) // Syst. Entomol. Vol.45. P.175–187. <https://doi.org/10.1111/syen.12386>
- Fikáček M., Yamamoto S., Matsumoto K., Beutel R.G., Maddison D.R. 2023. Phylogeny and systematics of Sphaeriusidae (Coleoptera:

- Myxophaga): minute living fossils with underestimated past and present-day diversity // *Syst. Entomol.* Vol.48. P.233–249. <https://doi.org/10.1111/syen.12571>
- Forbes W.T.M. 1926. Wing-folding patterns of Coleoptera // *J.N.Y. Entomol. Soc.* Vol.24. P.42–68, 91–139.
- Fraser N.C., Grimaldi D.A., Axsmith B.J., Heckert A.B., Liutkus-Pierce C., Smith D., Dooley A.C. Jr. 2017. The Solite Quarry – a window into life by a late Triassic lake margin // Fraser N.C., Sues H.-D. (eds.). *Terrestrial Conservation Lagerstätten – Windows into the Evolution of Life on Land.* Edinburgh: Dunedin. P.105–129.
- Ge S.-Q., Friedrich F., Beutel R.G. 2010. On the systematic position and taxonomic rank of the extinct myxophagan †*Haplochelus* (Coleoptera) // *Insect Syst. Evol.* Vol.41. P.329–338. <https://doi.org/10.1163/187631210X537385>
- Golovatch S.I. 2003. A review of the volvatory Polydesmida, with special reference to the patterns of volvation (Diplopoda) // *Afr. Invertebr.* Vol.44. P.39–60.
- Golubev V.K. 2000. The faunal assemblages of Permian terrestrial vertebrates from Eastern Europe // *Paleontol. J.* Vol.34. P.S211–S224.
- Handlirsch A. 1904. Über einige Insektenreste aus der Permformation Russlands // *Mém. Acad. imp. sci. St.-Petersbg.* Vol.16. No.5. P.1–8.
- Hasiotis S.T. 2000. The invertebrate invasion and evolution of Mesozoic soil ecosystems: the ichnofossil record of ecological innovations // *Paleontol. Soc. Papers.* Vol.6. P.141–170. <https://doi.org/10.1017/S1089332600000747>
- Heckman C.W. 1983. Comparative morphology of arthropod exterior surfaces with the capability of binding a film of air underwater // *Int. Revue ges. Hydrobiol.* Vol.68. P.715–736. <https://doi.org/10.1002/iroh.3510680515>
- Hinton H.E. 1967. On the spiracles of the larvae of the suborder Myxophaga (Coleoptera) // *Aust. J. Zool.* Vol.15. P.955–959. <https://doi.org/10.1071/ZO9670955>
- Hinton H.E. 1968. Spiracular gills // *Adv. Insect Physiol.* Vol.5. P.65–162.
- Jäch M.A. 1998. Annotated check list of aquatic and riparian/littoral beetle families of the world (Coleoptera) // Jäch M.A., Ji L. (eds). *Water Beetles of China.* Vol.2. Wien: Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein. P.25–42.
- Jałoszyński P., Yamamoto S., Takahashi Y. 2017. Discovery of a new Mesozoic species of the ancient genus *Lepicerus* (Coleoptera: Myxophaga: Lepiceridae), with implications for the systematic placement of all previously described extinct 'lepiceroids' // *Cretac. Res.* Vol.78. P.95–102. <https://doi.org/10.1016/j.cretres.2017.06.001>
- Jałoszyński P., Luo X.Z., Hammel J.U., Yamamoto S., Beutel R.G. 2020. The mid-Cretaceous †*Lepiceratus* gen. nov. and the evolution of the relict beetle family Lepiceridae (Insecta: Coleoptera: Myxophaga) // *J. Syst. Palaeontol.* Vol.18. P.1127–1140. <https://doi.org/10.1080/14772019.2020.1747561>
- Kirejtshuk A.G. 2009. A new genus and species of Sphaeriusidae (Coleoptera, Myxophaga) from Lower Cretaceous Burmese amber // *Denisia.* Vol.26. P.99–102.
- Kirejtshuk A.G., Poinar G. 2006. Haplochelidae, a new family of Cretaceous beetles (Coleoptera: Myxophaga) from Burmese amber // *Proc. Entomol. Soc. Wash.* Vol.108. P.155–164.
- Kirejtshuk A.G., Poinar G. 2013. On the systematic position of the genera *Lepiceroides* gen.n. and *Haplochelus* with notes on the taxonomy and phylogeny of the Myxophaga (Coleoptera) // Azar D., Engel M.S., Jarzembowsky E., Krogmann L., Nel A., Santiago-Blay J. (eds.). *Insect Evolution in an Amberiferous and Stone Alphabet.* Leiden: Brill. P.55–69.
- Kirejtshuk A.G., Prokin A.A. 2018. The position of the Palaeozoic genus *Tunguskagyryus* Yan, Beutel et Lawrence in the family Triaplidae sensu n. (Coleoptera, Archostemata: Schizophoroidea) // *Entomol. Rev.* Vol.98. P.872–882. <https://doi.org/10.1134/S0013873818070084>
- Kirejtshuk A.G., Prokin A.A., Ponomarenko A.G. 2023. New representative of the family Hydroscaphidae from Tunguska Basin, the boundary of the Permian and Triassic (Coleoptera, Myxophaga) with review on myxophagan fossil records // *Glob. J. Sci. Front. Res.* Vol.22. No.3. P.1–13. <https://doi.org/10.34257/GJSFRCVOL22IS3PG1>
- Kobayashi Y., Niikura K., Oosawa Y., Takami Y. 2013. Embryonic development of *Carabus insulicola* (Insecta, Coleoptera, Carabidae) with special reference to external morphology and tangible evidence for the subcoxal theory // *J. Morphol.* Vol.274. P.1323–1352. <https://doi.org/10.1002/jmor.20181>
- Lancaster J., Downes B.J. 2013. *Aquatic Entomology.* Oxford: Oxford University Press. 296 p.
- Lawrence J.F., Newton A.F. 1982. Evolution and classification of beetles // *Annu. Rev. Ecol. Syst.* Vol.13. P.261–290. <https://doi.org/10.1146/annurev.es.13.110182.001401>
- Lawrence J.F., Reichardt H. 1991. Torridincolidae (Myxophaga), Microsporidae (Myxophaga) (= Sphaeriidae), Hydroscaphidae (Myxophaga) // Stehr F.W. (ed.). *Immature Insects.* Vol.2. Dubuque, Iowa: Kendall/Hunt. P.302–304.
- Lawrence J.F., Ślipiński A. 2013. *Australian Beetles.* Vol.1: Morphology, Classification and Keys. Canberra: CSIRO. 576 p.
- Lawrence J.F., Ślipiński A., Seago A.E., Thayer M.K., Newton A.F., Marvaldi A.E. 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae // *Ann. Zool.* Vol.61. P.1–217. <https://doi.org/10.3161/000345411X576725>
- Lawrence J.F., Ślipiński A., Beutel R.G., Newton A.F. 2019. *Lepicerus* larva still unknown: a correction (Coleoptera: Lepiceridae, Phalacridae) // *Zootaxa.* Vol.4545. P.441–442. <https://doi.org/10.11646/zootaxa.4545.3.8>
- Li Y.D., Ślipiński A., Huang D.Y., Cai C. 2023. New fossils of Sphaeriidae from mid-Cretaceous Burmese amber revealed by confocal microscopy (Coleoptera: Myxophaga) // *Front. Earth Sci.* Vol.10. 901573. <https://doi.org/10.3389/feart.2022.901573>
- Lukashevich E.D. 2012. Pupae of Mesozoic *Oryctochlus* Kalugina, 1985 (Chironomidae: Podonominae), with description of two new species // *Fauna Norv.* Vol.31. P.159–165. <https://doi.org/10.5324/fn.v31i0.1400>
- Makarov K.V., Prokin A.A. 2015. About homology of *Haliplus* Latreille, 1802 larvae postanal process (Coleoptera, Haliplidae) // *Acta Entomol. Mus. Nat. Pragae.* Vol.55. P.879–881.
- Marchal-Papier F. 1998. Les insectes du Buntsandstein des Vosges (NE de la France). Biodiversité et contributions aux modalités de la crise biologique du Permo-Trias. PhD thesis, Strasbourg: Université Louis Pasteur. 177 p.
- Martynov A.V. 1937. [Permian fossil insects of Kargala and their relationships] // *Tr. Paleontol. Inst. AN SSSR.* Vol.7. No.2. P.1–92 [in Russian].
- Nechaev A.V. 1894. [The fauna of the Permian deposits of the eastern margin of European Russia] // *Tr. Obshch. estestvoispyt. imp. Kazan. univers.* Vol.27. No.4. P.1–515 [in Russian].
- Pedersen O., Colmer T.D. 2012. Physical gills prevent drowning of many wetland insects, spiders and plants // *J. Exp. Biol.* Vol.215. P.705–709. <https://doi.org/10.1242/jeb.065128>
- Perkins P.D., Bergsten J. 2019. New Myxophagan water beetles from Madagascar (Coleoptera: Torridincolidae, Hydroscaphidae) // *Zootaxa.* Vol.4657. P.57–96. <https://doi.org/10.11646/zootaxa.4657.1.2>
- Ponomarenko A.G. 1968. [Archostematan beetles from the Jurassic of Karatau (Coleoptera, Archostemata)]. In: Rohdendorf B.B. (ed.). *Yurskie nasekomye Karatau.* Moscow: Nauka. P.118–138 [in Russian].
- Ponomarenko A.G. 1969. [Historical development of archostematan beetles] // *Tr. Paleontol. Inst. AN SSSR.* Vol.125. P.1–240 [in Russian].
- Ponomarenko A.G. 1973. [On the division of the order Coleoptera into suborders]. In: Narchuk E.P. (ed.). [Problems of the Insect Paleontology]. *Doklady na 24-m ezhegodnom chtenii pamyati N.A. Kholodkovskogo,* 1971. Leningrad: Nauka. P.78–89 [in Russian].
- Ponomarenko A.G. 1977. [Introduction. Composition and ecological characteristic of Mesozoic Coleoptera. Suborder Adepfaga. Suborder Polyphaga. Polyphaga incertae sedis. Infraorder Staphyliniformia] // Arnol'di L.V., Zherikhin V.V., Nikritin L.M., Ponomarenko A.G. [Mesozoic Coleoptera]. *Tr. Paleontol. Inst. AN SSSR.* Vol.161. P.5–119 [in Russian; translated into English: 1992. Washington: Smithsonian Institution Libraries & NSF].
- Ponomarenko A.G. 1983. [Historical development of the order Coleoptera]. Doctoral thesis, Moscow: Paleontological Institute. [In Russian]
- Ponomarenko A.G. 2002. Superorder Scarabaeidea Laicharting, 1781. Order Coleoptera Linné, 1758. The beetles // Rasnitsyn A.P., Quicke D.L.J. (eds.). *History of Insects.* Dordrecht: Kluwer. P.164–176.
- Ponomarenko A.G. 2003a. The first beetles (Permosynidae, Coleoptera) from the upper Tatarian of European Russia // *Paleontol. J.* Vol.37. P.170–173.
- Ponomarenko A.G. 2003b. Ecological evolution of beetles // *Acta Zool. Cracov.* Vol.46 (Suppl.—Fossil Insects). P.319–328.

- Ponomarenko A.G. 2004. Beetles (Insecta, Coleoptera) of the Late Permian and Early Triassic // *Paleontol. J.* Vol.38. P.185–196.
- Ponomarenko A.G. 2008. New Triassic beetles (Coleoptera) from northern European Russia // *Paleontol. J.* Vol.42. P.600–606. <https://doi.org/10.1134/S0031030108060051>
- Ponomarenko A.G. 2011. New beetles (Insecta, Coleoptera) from Vyzniki locality, terminal Permian of European Russia // *Paleontol. J.* Vol.45. P.414–422. <https://doi.org/10.1134/S0031030111040095>
- Ponomarenko A.G. 2013. New beetles (Insecta, Coleoptera) from the latter half of the Permian of European Russia // *Paleontol. J.* Vol.47. P.705–735. <https://doi.org/10.1134/S0031030113070010>
- Ponomarenko A.G. 2015. New beetles (Insecta, Coleoptera) from the Nedubrovo Locality, terminal Permian or basal Triassic of European Russia // *Paleontol. J.* Vol.49. P.39–50. <https://doi.org/10.1134/S0031030115010098>
- Ponomarenko A.G. 2021. Permian triaplids (Coleoptera, Triaplidae), yet another group of Mesozoic beetles from the terminal Permian // *Paleontol. J.* Vol.55. P.650–661. <https://doi.org/10.1134/S0031030121050130>
- Ponomarenko A.G., Prokin A.A. 2015. Review of paleontological data on the evolution of aquatic beetles (Coleoptera) // *Paleontol. J.* Vol.49. P.1383–1412. <https://doi.org/10.1134/S0031030115130080>
- Ponomarenko A.G., Volkov A.N. 2013. *Ademosynoides asiaticus* Martynov, 1936, the earliest known member of an extant beetle family (Insecta, Coleoptera, Trachypachidae) // *Paleontol. J.* Vol.47. P.601–606. <https://doi.org/10.1134/S0031030113060063>
- Prokin A.A., Bashkuev A.S. 2021. *Trialarva coburgensis* gen. et sp. nov., a remarkable fossil holometabolan larva (Insecta: Coleoptera) from the Triassic of Germany // *PalZ.* Vol.95. P.55–60. <https://doi.org/10.1007/s12542-020-00527-6>
- Prokin A.A., Petrov P.N., Wang B., Ponomarenko A.G. 2013. New fossil taxa and notes on the Mesozoic evolution of Liadytidae and Dytiscidae (Coleoptera) // *Zootaxa.* Vol.3666. P.137–159. <https://doi.org/10.11646/zootaxa.3666.2.2>
- Prokin A.A., Kirejtshuk A.G., Ponomarenko A.G. 2015. On some Permian and Triassic larvae of Holometabola: beetles or not? // *Acta Entomol. Mus. Nat. Pragae.* Vol.55. P.882–884.
- Prokin A.A., Ponomarenko A.G., Kirejtshuk A.G. 2019. Description of a larva of *Kargalarva permosialis* gen. et sp. nov. (Coleoptera: Schizophoromorpha) from the Kargala fossil site // *Paleontol. J.* Vol.53. P.282–286. <https://doi.org/10.1134/S0031030119030110>
- Qvarnström M., Fikáček M., Wernström J.V., Huld S., Beutel R.G., Arriaga-Varela E., Ahlberg P.E., Niedzwiedzki G. 2021. Exceptionally preserved beetles in a Triassic coprolite of putative dinosauriform origin // *Curr. Biol.* Vol.31. P.3374–3381. <https://doi.org/10.1016/j.cub.2021.05.015>
- Reichardt H. 1973. A critical study of the suborder Myxophaga, with a taxonomic revision of the Brazilian Torridincolidae and Hydroscaphidae (Coleoptera) // *Arq. Zool.* Vol.24. P.73–162. <https://doi.org/10.11606/issn.2176-7793.v24i2p73-162>
- Riek E.F. 1976. New Upper Permian insects from Natal, South Africa // *Ann. Natal Mus.* Vol.22. P.755–789. https://hdl.handle.net/10520/AJA03040798_613
- Schram F.R. 1986. Crustacea. New York: Oxford University Press. 606 p.
- Sennikov A.G., Golubev V.K. 2017. Sequence of Permian tetrapod faunas of Eastern Europe and the Permian–Triassic ecological crisis // *Paleontol. J.* Vol.51. P.600–611. <https://doi.org/10.1134/S0031030117060077>
- Sharov A.G. 1953. [First record of Permian larva of alderflies (Megaloptera) from Kargala] // *Doklady AN SSSR (N.S.).* Vol.89. P.731–732 [in Russian].
- Shcherbakov D.E. 2008. On Permian and Triassic insect faunas in relation to biogeography and the Permian–Triassic crisis // *Paleontol. J.* Vol.42. P.15–31. <https://doi.org/10.1134/S0031030108010036>
- Shcherbakov D.E. 2022. New Dymorphoptilidae (Cicadomorpha) from the end-Permian and Middle Jurassic of Siberia: earliest evidence of acoustic communication in Hemiptera and the latest find of the family // *Russian Entomol. J.* Vol.31. P.108–113. <https://doi.org/10.15298/rusentj.31.2.02>
- Shcherbakov D.E., Vinn O., Zhuravlev A.Y. 2021. Disaster microconchids from the uppermost Permian and Lower Triassic lacustrine strata of the Cis-Urals and the Tunguska and Kuznetsk basins (Russia) // *Geol. Mag.* Vol.158. P.1335–1357. <https://doi.org/10.1017/S0016756820001375>
- Shepard W.D., Clavier S., Cerdan A. 2020. A generic key to the known larval Elmidae (Insecta: Coleoptera) of French Guiana // *Pap. Avulsos Zool.* Vol.60. Special issue. Art.e202060(s.i).15 <http://doi.org/10.11606/1807-0205/2020.60.special-issue.15>
- Spangler P.J. 1990. A revision of the Neotropical aquatic beetle genus *Stegoelmis* (Coleoptera: Elmidae) // *Smithson. Contrib. Zool.* Vol.502. P.1–52. <https://doi.org/10.5479/si.00810282.502>
- Steffan A.W. 1964. Torridincolidae, coleopterorum nova familia e regione aethiopica // *Entomol. Z.* Vol.74. P.193–200.
- Thorpe W.H. 1950. Plastron respiration in aquatic insects // *Biol. Rev.* Vol.25. P.344–390. <https://doi.org/10.1111/j.1469-185X.1950.tb01590.x>
- Vanin S.A., Costa C. 2001. Description of immature stages of *Claudiella ingens* Reichardt & Vanin, 1976 and comparative notes on other Torridincolidae (Coleoptera, Torridincolidae) // *Aquat. Insects.* Vol.23. P.1–10. <https://doi.org/10.1076/aqin.23.1.1.4925>
- Volkov A.N. 2013. New species of Triaplidae from the Babii Kamen locality (Kuznetsk Basin) // *Paleontol. J.* Vol.47. P.94–97. <https://doi.org/10.1134/S0031030113010140>
- Yan E.V., Strelnikova O.D. 2022. Early evolution of beetles of the suborder Polyphaga (Insecta: Coleoptera) at the Permian–Triassic boundary // *Paleontol. J.* Vol.56. P.268–279. <https://doi.org/10.1134/S0031030122030169>
- Yan E.V., Beutel R.G., Lawrence J.F. 2018. Whirling in the late Permian: ancestral Gyridae show early radiation of beetles before Permian–Triassic mass extinction // *BMC Evol. Biol.* Vol.18. 33. <https://doi.org/10.1186/s12862-018-1139-8>
- Zheng D., Chang S.C., Wang H., Fang Y., Wang J., Feng C., Xie G., Jarzembowski E.A., Zhang H., Wang B. 2018. Middle-Late Triassic insect radiation revealed by diverse fossils and isotopic ages from China // *Science advances.* Vol.4. Art.eaat1380. <https://doi.org/10.1126/sciadv.aat1380>