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A new species, *Lochriea monocarinata* n. sp., and its position in the morphospace of the genus *Lochriea* Scott, 1942 (Conodonta, Mississippian)

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ABSTRACT

KEY WORDS Conodonts, morphology, Carboniferous, Serpukhovian, new species. The new species of the Mississippian conodonts *Lochriea monocarinata* n. sp. extends the diversity of the ornamented representatives of the genus *Lochriea* Scott, 1942. *Lochriea monocarinata* n. sp. differs from its close relatives by the presence of a nodose ridge only on the inner (caudal) part of the asymmetrical basal cup. The range of the new species, restricted to the *Lochriea ziegleri* Zone, allows it to be used as an auxiliary biostratigraphic marker of the lower Serpukhovian.

RÉSUMÉ

Une espèce nouvelle, Lochriea monocarinata n. sp., et sa position dans le morphoespace du genre Lochriea Scott, 1942 (Conodonta, Mississippien).

MOTS CLÉS Conodontes, morphologie, Carbonifère, Serpukhovian, espèce nouvelle. La nouvelle espèce de conodontes du Mississippian *Lochriea monocarinata* n. sp. élargit la diversité des représentants ornementés du genre *Lochriea* Scott, 1942. *Lochriea monocarinata* n. sp. diffère de ses proches parents par la présence d'une crête nodosée uniquement sur la partie interne (caudale) de la coupe basale asymétrique. L'aire de répartition de la nouvelle espèce, limitée par la zone à *Lochriea ziegleri*, permet de l'utiliser comme marqueur biostratigraphique auxiliaire du Serpukhovien inférieur.



Fig. 1. — Location of the studied sections (\star): **A**, general geographical position of the studied area; **B**, location of the sections: **1**, Kamenka section; **2**, Izyayu section; **3**, Kozhim section; **4**, Bolshaya Nadota section.

INTRODUCTION

Conodonts are a group of small free-swimming, probably nektic or nektonplanktic, marine animals (Briggs *et al.* 1983) that became extinct during the latest Triassic-earliest Jurassic (Du *et al.* 2023). The only mineralised parts of conodonts are tooth-like phosphate elements arranged in a bilaterally subsymmetrical feeding apparatus. Current conodont taxonomy is based on the structure of the apparatus and the morphology of the conodont elements (e.g. Dzik 1976; Sweet 1988). Due to their rapid morphological evolution, conodont elements are widely used in Palaeozoic and Triassic biostratigraphy, including part of the definition of the GSSPs (Global Boundary Stratotype Sections and Points) in the International Chronostratigraphic Scale.

According to Nemyrovska et al. (2006), the conodont genus Lochriea appeared in the early Viséan, and Lochriea saharae Nemyrovska, Perret-Mirouse & Weyant, 2006 is the oldest known species of the genus. Another genus concept includes "Lochriea" symmutata (Rhodes, Austin & Druce, 1969) and "L." homopunctata (Ziegler, 1960) to the genus Lochriea (Atakul-Özdemir et al. 2012). In this case the oldest species of the genus is "Lochriea" symmutata, which appears in the middle Tournaisian (Zhuravlev 2003). The last representatives of the genus Lochriea are known from the early Pennsylvanian (e.g. Kulagina et al. 1992; Mizuno 1997; Sanz-López et al. 2013; Hu et al. 2019). Some species of this genus compose the basis of the conodont zonation of the Viséan-Serpukhovian interval (Mississippian): lower Viséan Lochriea commutata Zone, upper Viséan Lochriea mononodosa Zone and Lochriea nodosa Zone, lower Serpukhovian Lochriea ziegleri Zone and Lochriea cruciformis Zone (Metcalfe 1981; Belka 1985; Skompski 1996; Qi & Wang 2005; Vevel et al. 2017; Sudar et al. 2018). The first appearance datum (FAD) of Lochriea ziegleri Nemirovskaya, Perret & Meischner, 1994, is considered a probable biostratigraphic marker of the base of Serpukhovian Stage (Richards 2010; Richards et al. 2011, 2017; Sevastopulo & Barham 2014; Nikolaeva et al. 2020).

The genus Lochriea has been established as multielement taxon (Scott 1942; von Bitter et al. 2022). However, specieslevel taxonomy is based solely on the morphology of P1 elements (e.g., Nemirovskaya et al. 1994; Nemyrovska et al. 2006; Qi et al. 2018). Therefore, the morphology of P1 elements has attracted the most attention from researchers (e.g. Barham et al. 2015). Combinations of traits of P1 elements allow for distinguishing a number of species and proposing the phylomorphogeny of the genus (e.g. Barham et al. 2015; Vevel et al. 2017; Qi et al. 2018). Twelve species of the genus are known, and several forms have been described in open nomenclature (e.g. Barham et al. 2015). Some species similar to Lochriea have debated affinities ("Lochriea" symmutata, "L." homopunctata, "L." mermaidus (Austin & Husri, 1975), "L." lineatus (Austin & Husri, 1975), Pseudognathodus posadachaconae Sanz-López, Blanco-Ferrera & Miller, 2018) (see Atakul-Özdemir et al. 2012; Sanz-López et al. 2018 for discussion). In any case the P1 elements of these discussed species compose a different morphospace close to that of Protognathodus, with a smooth cup or a cup ornamented with a few small nodes, rows of nodes, or short costae (e.g. Sanz-López et al. 2018).

The early representatives of the genus Lochriea (L. saharae, L. commutata (Branson & Mehl, 1934), L. scotiaensis (Globensky, 1967), L. cracoviensis (Belka, 1985)) show a simple morphology of P1 elements similar to that of Bispathodus or early Protognathodus. Advanced species of Lochriea (L. monocostata (Pazukhin & Nemirovskaya in Kulagina et al., 1992), L. costata (Pazukhin & Nemirovskaya in Kulagina et al., 1992), L. ziegleri, L. senckenbergica Nemirovskaya, Perret &



FIG. 2. — Correlation of the key sections of the uppermost Viséan-Serpukhovian interval in the North Urals and Cis-Urals (Vevel *et al.* 2018; Zhuravlev *et al.* 2023). Abbreviations: **m**, mudstone; **w**, wackestones; **p**, packstone; **g**, grainstone; **f**, floatstone; **FOD**, first occurrence datum; **G**., *Gnathodus* Pander, 1856; *L*., *Lochriea* Scott, 1942. The **stars** mark occurrences of *Lochriea monocarinata* n. sp.

Meischner, 1994, *L. mononodosa* (Rhodes, Austin & Druce, 1969), *L. nodosa* (Bischoff, 1957), *L. cruciformis* (Clarke, 1960), *L. multinodosa* (Wirth, 1967)) from the Late Viséan and Serpukhovian show complication of morphology, mainly in the ornamentation of the basal cup (e.g. Qi *et al.* 2018).

This study aims to describe a new species of advanced *Lochriea* with an ornamented basal cup and to characterise the position of this species in the morphospace of the genus.

MATERIAL AND METHODS

This study is based on the author's conodont collections from the late Mississippian key sections of the northern Cis-Urals and Subpolar Urals (Figs 1; 2), and analyses of published data (Metcalfe 1981; Kulagina *et al.* 1992; Nemirovskaya *et al.* 1994, Skompski *et al.* 1995; Belka & Lehmann 1998; Nemyrovska *et al.* 2006; Qi *et al.* 2014, 2018; Barham *et al.* 2015; Richards *et al.* 2017; Wang *et al.* 2018; Nikolaeva *et al.* 2020, etc.).

The upper Viséan-Serpukhovian carbonate platform deposits cropping out in the northern Cis-Urals and Subpolar Urals regions yield diverse conodonts including *Lochriea* species (e.g. Zhuravlev 2003; Vevel *et al.* 2017; Zhuravlev *et al.* 2023). In total, about 480 P1 elements represent *Lochriea* species in the studied collections. About 300 of them belong to advanced *Lochriea* species with ornamentation on the basal cup. *Lochriea commutata* represents about 25% of the total P1 elements of *Lochriea* in the studied collections, but each highly ornamented species composes 2-15% of the total P1 elements of the genus.

The Figure 3 explains the terminology used in this study. In general, P1 elements of the genus Lochriea show a carminiscaphate morphology with the basal cup located in the middle or posterior (dorsal) part of the element. The cup ornamentation can be represented by node(s), costa, and ridges. Specific terminology is used here to distinguish variations in cup ornamentation in advanced Lochriea. The term costa is used to refer to swell-like elongated, smooth or poorly ornamented with smooth nodes structures. The term ridge is used for elongated structures consisting of a series of crenulated nodes arranged on the raised area. In some cases, the nodes form an array covering almost the entire surface of the basal cup (e.g. Lochriea multinodosa). The ornamentation of the outer (rostral) and inner (caudal) parts of the cup and the morphology of the carina are the main specific traits of the members of the genus Lochriea. The terms for the orientation of the elements (Fig. 3) follow Purnell et al. (2000).

MORPHOSPACE OF THE P1 ELEMENTS OF *LOCHRIEA*

Various combinations of basal cup position, cup ornamentation type and distribution, and carina morphology make up the morphospace of P1 elements of the genus (Fig. 4). The subdivision of the morphospace is conventional due to the presence of numerous transitional forms (Fig. 5; see also Barham *et al.* 2015; Qi *et al.* 2014, 2018).

The cup ornamentation can be divided into the following types: smooth cup, cup ornamented with node (nodes) (e.g. Fig. 5G, L, Q, X), cup ornamented with costa (costae) (e.g. Fig. 5K, Y), cup ornamented with ridge (ridges), and cup ornamented with numerous nodes (nodose platform). The smooth cup is characteristic of early Lochriea, but the ornamented cup is characteristic of advanced Lochriea. The node, costa or ridge can ornament the cup on both sides (rostral and caudal) or only on the inner (caudal) side (Fig. 4). The most taxonomically diverse morphological group, consisting of three species (Lochriea cruciformis, L. senckenbergica, and L. ziegleri), shows ridges ornamenting both sides of the basal cup (Figs 4; 5A-F, H, I, M). The ornamentation can be located in the middle part of the cup (Lochriea cruciformis and L. senckenbergica), or the posterior (dorsal) part of the cup (Lochriea ziegleri).

The carina can be narrow or wide in the posterior part. The wide posterior carina is characteristic of species with a smooth basal cup (*Lochriea scotiaensis* and *L. cracoviensis*) (Fig. 4).

A posterior (dorsal) position of the basal cup is found in most species of *Lochriea*. Some early representatives of the genus (*Lochriea saharae*, *L. cracoviensis*) show a basal cup located near the middle part of the P1 element. The posterior displacement of the basal cup and the increasing asymmetry of the basal cup in *Lochriea commutata* during ontogeny is remarkable (Gatovskii & Zhokina 2014). This ontogenetic transformation probably repeats the phylogenetic transformation in the lineage from *Lochriea saharae* to *Lochriea commutata*.

The early *Lochriea* species show the symmetry between the dextral and sinistral P1 elements (Class II symmetry of Lane 1968). Most advanced *Lochriea* demonstrate a weak asymmetry between the dextral and sinistral P1 elements (transition from Class II to Class III symmetry). Only *Lochriea senckenbergica* shows a distinct asymmetry between the dextral and sinistral P1 elements (Class III symmetry of Lane 1968) (Vevel *et al.* 2017: fig. 6).

The morphospace of the P1 elements allows the prediction of the existence of a number of new, previously unknown species. One of these species, *Lochriea monocarinata* n. sp. is described here. It is noteworthy that forms corresponding to the new species were first characterised by Bahram *et al.* (2015) as specimens with complex ornament on only one side of the P1 element. P1 elements of *L. monocarinata* n. sp. represent about 2% of all studied specimens of the genus in the author's collections. Another probable new form with P1 elements bearing a nodose platform only on the inner part of the basal cup remains hypothetical (marked as *Lochriea* sp. B? in Fig. 4).

The morphological types represented in the morphospace (Fig. 4) are linked to each other by a large number of transitional forms. The morphological transitions are known between *Lochriea saharae* and *L. commutata* (Nemyrovska *et al.* 2006), as well as between *L. commutata* and *L. cracov*-



Fig. 3. - Morphology of the P1 element of Lochriea Scott, 1942 and the terms for the orientation of the elements (Purnell et al. 2000).

iensis (Belka 1985) in early *Lochriea*. Transitions between *L. commutata* and *L. monocostata* (e.g. Qi *et al.* 2018: fig. 4), between *L. commutata* and *L. costata* (e.g. Barham *et al.* 2015: fig. 10.6), between *L. commutata* and *L. mononodosa* (Fig. 5O, T) (see also Barham *et al.* 2015: fig. 13) connect early and advanced *Lochriea*. Advanced *Lochriea* show morphological transitions between *L. mononodosa* and *L. monocostata* (Qi *et al.* 2018: fig. 4); *L. mononodosa* and *L. monocostata* (e.g. Barham *et al.* 2015: fig. 10.1a, b); *L. mononodosa* and

L senckenbergica (e.g. Barham et al. 2015: figs 11.7, 11.12); L. mononodosa and L. ziegleri (e.g. Barham et al. 2015: figs 10.8, 11.11); L. mononodosa and L. cruciformis (e.g. Barham et al. 2015: figs 11.4, 11.5); L. nodosa and L. costata (Barham et al. 2015: fig. 10.2a, b; Kullmann et al. 2008: figs. 9.1, 9.5; Nikolaeva et al. 2009: fig. 6J); L. nodosa and L. senckenbergica (e.g. Qi et al. 2018: fig. 4); L. nodosa and L. ziegleri (e.g. Qi et al. 2018: fig. 4; Barham et al. 2015: figs 10.4a, b, 10.7, 10.9, 10.11, 11.9, 11.13; Nemirovskaya



Fig. 4. — Morphospace of the P1 elements of Lochriea Scott, 1942.

et al. 1994: pl.2, fig. 6); L. nodosa and L. cruciformis (e.g. Barham et al. 2015: fig. 10.3a,b; Nemyrovska 2005: pl.8, fig. 9); L. nodosa and L. multinodosa (e.g. Kullmann et al. 2008: fig. 10.3; Nemyrovska 2005: pl. 8, fig. 15). Also, transitional forms are known between L. monocostata and L. costata (e.g. Qi et al. 2018: fig. 4; Nikolaeva et al. 2020: fig. 12C as L. monocostata); L. costata and L senckenbergica (e.g. Qi et al. 2018: fig. 4); L senckenbergica and L. ziegleri (e.g. Nemirovskaya et al. 1994: pl. 2, fig. 14); L. ziegleri and L. cruciformis (e.g. Barham et al. 2015: figs 10.5, 10.10); L. senckenbergica and L. cruciformis (Fig. 5E, F). These morphological transitions complicate the taxonomic diagnostics of Lochriea species, especially among the advanced Lochriea (e.g. Herbig 2017).

The morphological diversity, the known problems with the holotypes of a number of species of *Lochriea*, and the lack of knowledge about the apparatus composition of most species prevent an adequate taxonomic revision of this genus (Alekseev & Nikolaeva 2019). The complete taxonomic revision of the genus is beyond the scope of this paper.

SYSTEMATIC PALAEONTOLOGY

Class CONODONTA Pander, 1856 Order OZARKODINIDA Dzik, 1976 Suborder OZARKODININA Dzik, 1976 Family Spathognathodontidae Hass, 1959

Genus Lochriea Scott, 1942

TYPE SPECIES. — Lochriea montanaensis Scott, 1942 by original designation.

Lochriea monocarinata n. sp. (Fig. 5N, P, R, S, U-W, Z)

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Gnathodus nodosus - Metcalfe 1981: 47, pl. 7, fig. 3.

Paragnathodus monocostatus - Kulagina et al. 1992: pl. XXIX, fig. 7.

Lochriea sp. - Barham et al. 2015: 15, figs 11.1, 11.12, 11.4, 11.5, 11.7.

Lochriea sp. - Wang et al. 2018: 438, figs 3.53, 3.54.

Lochriea monocostata - Nikolaeva et al. 2020: fig. 12J.

ETYMOLOGY. — According to the ornamentation of basal cup represented by a single ridge.

TYPE MATERIAL. — Russia • North Cis-Urals, Tchenyshev Ridge, Izyayu section; 65°33'9.53"N, 58°38'50.32"E; Mississippian, early Serpukhovian, *L. ziegleri* Zone; holotype: specimen 445/12, sample Iz4-52/98 (Fig. 5Z), housed in Chernov Museum of Institute of Geology FRC Komi SC UrB RAS, Syktyvkar.

TYPE LOCALITY. — Izyayu section, Tchenyshev Ridge, North Cis-Urals, Russia (65°33'9.53"N, 58°38'50.32"E).

TYPE AGE. — Mississippian, early Serpukhovian, *L. ziegleri* Zone.

DIAGNOSIS. — Species of *Lochriea* with P1 element bearing the nodose ridge on the inner (caudal) part of the asymmetrical basal cup.

MATERIAL EXAMINED. — Nine specimens from the Serpukhovian of North Urals and North Cis-Urals.

DISTRIBUTION. — The new species is known from the lower Serpukhovian (*L. ziegleri* Zone) of the North Cis-Urals, Sub-Polar Urals, South Urals (Eastern Laurussia), Rhenish Mountains (Wang *et al.* 2018), northwest Ireland (Barham *et al.* 2015) and Craven Lowlands of northern England (Metcalfe 1981) (Southern Laurussia).

DESCRIPTION

The carminiscaphate P1 element has a basal cap located near the posterior (dorsal) end. Carina is high with denticles of almost uniform height. Upper part of denticles in posterior part of carina is broad and bears pustulation. Cup is asymmetrical and bears the nodose crenulated ridge on the inner (caudal) side.

Sinistral and dextral P1 elements compose an almost symmetrical pair (transition from Class II symmetry to Class III symmetry). The dextral elements are characterised by less cup asymmetry and a ventrally displaced nodose ridge (Fig. 6E-G). The sinistral elements show a more developed ridge ornamentation compared to the dextral elements at the same stage of ontogeny (Fig. 6A-D). Sinistral P1 elements have isometric nodes on ridge, but dextral P1 elements have elongated nodes on ridge. This difference in node shape probably provides better occlusion of the sinistral and dextral elements. The asymmetry of the sinistral and dextral P1 elements ensures that they are occluded in the apparatus in a "dextral in front of the sinistral" pattern (Fig. 6H). The apparatus composition of the new species has not yet been reconstructed. Lochriea monocarinata n. sp. probably shares S, M, and P2 elements with other advanced representatives of the genus *Lochriea* (e.g. Fig. 5AA).

Remarks

The new species differs from *Lochriea monocostata* by distinct crenulate nodose ornamentation on the inner ridge. Transitional forms from L. monocostata to L. monocarinata n. sp. possess weak nodose ornamentation of the costa consisting of one or two small and smooth nodes (Fig. 5Y) (see also Nemirovskaya et al. 1994: pl. 2, fig. 3; Nemyrovska et al. 2011: pl. 2, fig. 2; Nikolaeva et al. 2020: fig. 12A). The morphological transitions from L. mononodosa to L. monocarinata n. sp. (Fig. 5Q) and from L. monocarinata n. sp. to L. ziegleri (Fig. 5]) also occur. Lochriea monocarinata n. sp. can be distinguished from L. mononodosa and L. monocostata by the presence of at least three crenulate nodes forming the ridge. The ornamentation of the P1 elements of *L. monocarinata* n. sp. in the early stages of ontogeny is almost identical to that of L. monocostata or L. mononodosa. If the nodes are crenulated, specimens with a ridge decorated with two nodes in the early stages of ontogeny can be identified as L. monocarinata n. sp. (e.g. Figs 5Q; 6A, E).



Fig. 5. — Some advanced Lochriea from the Serpukhovian (Lochriea ziegleri Zone) of North of Urals and Cis-Urals region: A, Lochriea ziegleri Nemirovskaya, Perret-Mirouse, Meischner, 1994, specimen 145/24, sample lz4-51/98, Izyayu section; B, Lochriea ziegleri Nemirovskaya, Perret & Meischner, 1994, specimen 145/19, sample K99-21/22, Kamenka section; C, Lochriea senckenbergica Nemirovskaya, Perret & Meischner, 1994, specimen 145/22, sample 125-19/22, Kamenka section; D, Lochriea ziegleri Nemirovskaya, Perret & Meischner, 1994, specimen 145/20, sample K99-21/22, Kamenka section; E, Lochriea senckenbergica Nemirovskaya, Perret & Meischner, 1994, specimen 145/20, sample K99-21/22, Kamenka section; E, Lochriea senckenbergica Nemirovskaya, Perret & Meischner, 1994-Lochriea cruciformis (Clarke, 1960) transition, specimen 145/23, sample Iz4-52/98, Izyayu section; F, Lochriea senckenbergica Nemirovskaya, Perret & Meischner, 1994 – Lochriea cruciformis (Clarke, 1960) transition, specimen 145/27, sample Iz4-53/98, Izyayu section; G, Lochriea monondosa (Rhodes, Austin & Druce, 1969), specimen 145/15, sample N2-1-11/99, Bolshaya Nadota section; H, Lochriea sp., specimen 145/12,

CONCLUDING REMARKS

The wide geographical distribution in the narrow stratigraphic interval (*L. ziegleri* Zone) of the forms described here as *Lochriea monocarinata* n. sp. suggests that these forms are not teratomorphic, but represent the evolutionary stage of advanced *Lochriea*. The presence of dextral and sinistral elements with morphological features of the new species also supports the validity of this taxon. The position of P1 elements of *L. monocarinata* n. sp. in the morphospace of the genus allows the author to assume evolutionary or at least morphogenetic relationships of this species with *L. monocarinata* n. sp. restricted by the *L. ziegleri* Zone allows this species to be used as an auxiliary biostratigraphic marker of the lower Serpukhovian.

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FIG. 6. — Morphological schemes of sinistral (A-D) and dextral (E-G) P1 elements of *Lochriea monocarinata* n. sp. and scheme of probable occlusion of sinistral (red) and dextral (green) elements (H). The line drawings are based on the SEM microphotographs (see Fig. 5). D, holotype, specimen 445/12. Abbreviations: d, dextral; s, sinistral.

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