A new record of the enigmatic mollusc *Jinonicella* from the Silurian of the Carnic Alps, Austria

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Abstract. The small enigmatic mollusc *Jinonicella kolebabai* Pokorný, 1978 is described from the upper Silurian Cardiola Formation at the Rauchkofel Süd section of the Carnic Alps, Austria. The associated conodonts suggest a late Ludlow (Ludfordian) *Polygnathoides siluricus* conodont Zone. Previous Silurian records of *Jinonicella* are known from the Wenlock to Ludlow of the Czech Republic, USA, Gotland of Sweden and the Carnic Alps of Austria. The wide distribution of this taxon across different climatic zones and widely separated areas in the Silurian is problematic, and it is unclear whether *Jinonicella* was present in high-latitude areas before the end-Ordovician cooling and mass extinction or was dispersed during the Silurian. Possible planktotrophy in *Jinonicella* and Silurian ocean circulation patterns may explain the dispersal, but within the framework of current palaeogeographical reconstructions the model does not adequately explain an equatorial to polar distribution of other contemporaneous benthic faunas from these areas.

Key words: Silurian, Carnic Alps, problematic mollusc, *Jinonicella*, palaeogeography.

INTRODUCTION

The minute and striking shells of the enigmatic mollusc *Jinonicella* are known from the Middle Ordovician to the Devonian. Typically all these shells are attributed to the species *J. kolebabai* Pokorný, 1978, but the taxon probably includes several species as few and often poorly preserved specimens preclude close comparison on the species level (Gubanov et al. 2017). Nevertheless, the conservative size and morphology over such a long time span is noteworthy. The oldest *J. kolebabai* was reported from the Middle Ordovician of Ukraine and Belarus (Hynda 1986). In the Late Ordovician it has been reported from the Lesieniec 1 borehole and the Mójcza Limestone in Poland (Dzik 1994a, 1994b). The record of this peculiar fossil is more extensive in the Silurian, with reports from the Llandovery of Utah, USA (Gubanov et al. 2017), Wenlock of Gotland, Sweden (Peel & Jeppsson 2006), and Ludlow of Bohemia, Czech Republic (Pokorný 1978a) and the Carnic Alps, Austria (Dzik 1994b). It is also present in the late middle Devonian of Bohemia (Budil 1995) and Pennsylvania, USA (Chamberlain et al. 2016). *Jinonicella* sp. has been reported from the Late Devonian strata of the Refrath 1 borehole, Rhenish Massif, western Germany (Piecha 2004).

This peculiar microfossil was originally described and known earlier from the Ludlow of the Prague Basin, Czech Republic (Pokorný 1978a). The taxonomic relationship of *Jinonicella*, as well as the broadly similar microfossil *Janospira* Fortey & Whittaker, 1976, described from the Ordovician of Spitsbergen, is obscure; whether it is a polychaete (Yochelson 1977), an archaeo-gastropod (Pokorný 1978a, 1978b), a monoplacophoran, i.e. a possible successor of the Cambrian *Yochelcionella* (Runnegar 1977), or derived from the ribeiriid rostroconch molluscs (Peel 2006; Peel & Jeppsson 2006).

Residues from the Silurian (Wenlock–Pridoli) cephalopod limestone of the Cardiola Formation of the central part of the Austrian Carnic Alps extracted through processing in a weak acid yielded specimens of *J. kolebabai* Pokorný, occurring within the *Polygnathoides siluricus* Biozone (Ludlow, Ludfordian) of the Rauchkofel Süd section (Fig. 1). This is the second

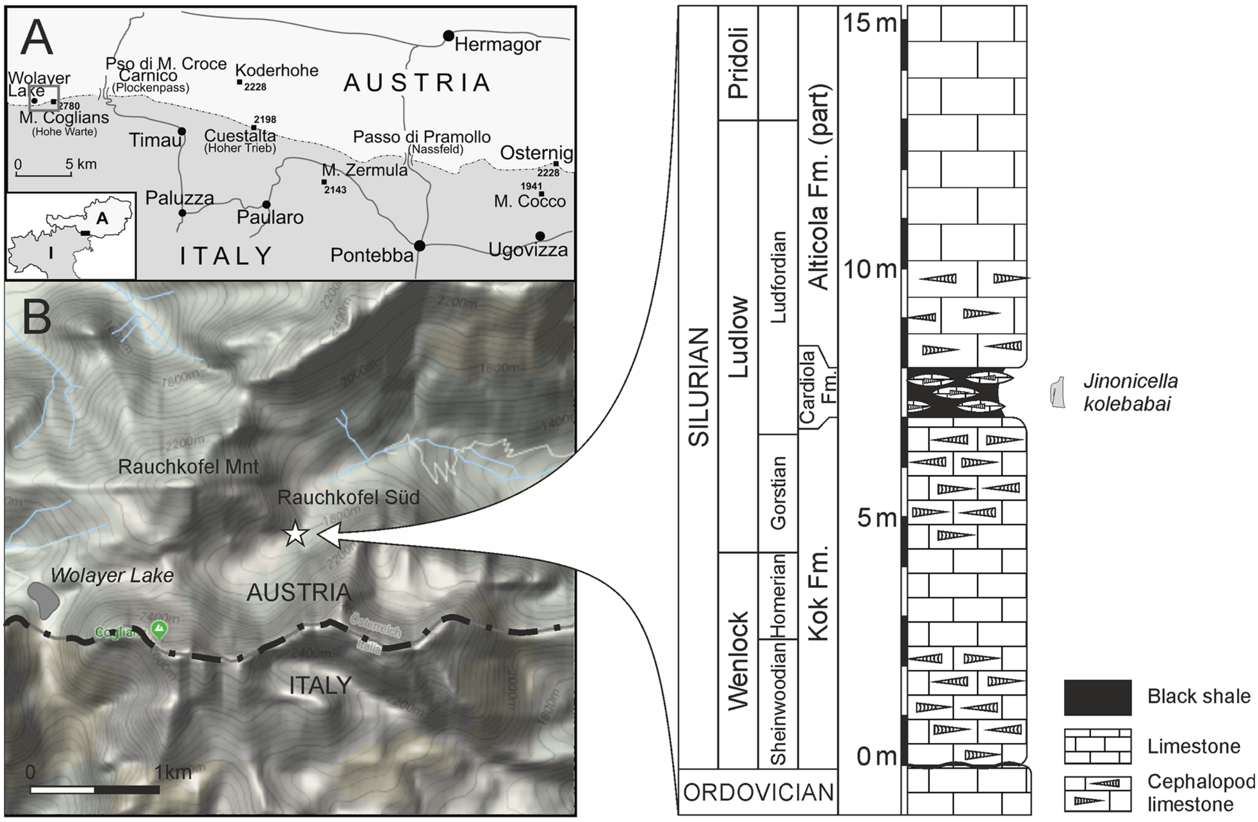

Fig. 1. A, location of the Carnic Alps. **B**, location map of the Rauchkofel Süd section (white star) showing the stratigraphy and the position of *Jinonicella kolebabai* in the succession.

report of *Jinonicella* from the Carnic Alps, albeit the previous record was from the slightly older Kok Formation (Dzik 1994b).

MATERIAL AND GEOLOGICAL SETTING

The Carnic Alps are located across the Austrian–Italian border. The Silurian succession is rather thin in the Carnic Alps with a total thickness of 20–60 m (Corradini et al. 2015). Deposits are ranging from shallow-water carbonate facies in the west to deep-water graptolitic shales and cherts in the east (Wenzel 1997). The studied area lies within the Austrian Carinthia province (Fig. 1). The Silurian succession is here about 20 m thick and is represented by the shallow-water Wolayer facies consisting of, in ascending order, the Kok, Cardiola and Alticola formations. Most of the Llandovery strata are lacking due to a significant stratigraphic gap between the Ordovician and Silurian sediments (Corradini et al. 2015).

The samples with *J. kolebabai* were collected from limestones of the Cardiola Formation on the southern slope of the Mount Rauchkofel in the Austrian Carnic Alps (Fig. 1). The Cardiola Formation (Fig. 2) is up to 4 m thick and is composed of dark grey to black shales intercalated with thin fossiliferous limestone layers. In the Rauchkofel Süd section, the Cardiola Formation is 30–50 cm thick and poorly exposed. The Cardiola Formation is sandwiched between the two massive limestone units of the Kok and Alticola formations (Fig. 1). These three units are highly fossiliferous and correspond to the 'Orthoceras limestones', now referred to as the Cephalopod Limestone Biofacies (e.g. Ferretti & Kříž 1995; Kříž & Bogolepova 1995). The Cardiola Formation contains a rich fauna of cephalopods, bivalves and gastropods, trilobites, crinoids, brachiopods, ostracods, conodonts as well as chitinozoans (e.g. Schönlaub 1970; Schönlaub & Kreutzer 1994; Brett et al. 2009; Corradini et al. 2015; Ferretti et al. 2016). Additionally, the processed samples from the Cardiola Formation of Rauchkofel Süd also yielded vertebrate remains.

The specimens studied in this paper are stored in the Palaeontological collections, Museum of Evolution, Uppsala University, Sweden (PMU).

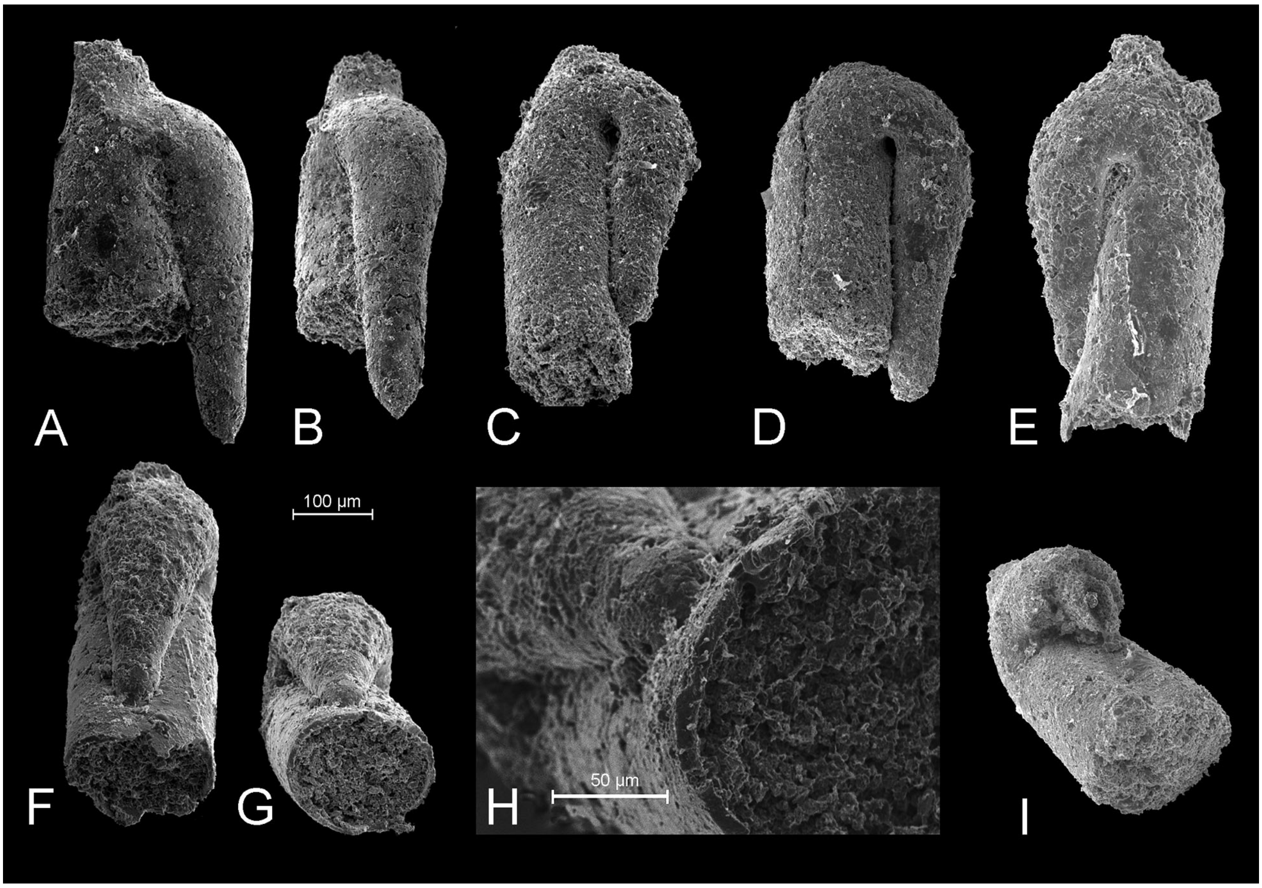

Fig. 2. *Jinonicella kolebabai* Pokorný, 1978. **A–E**, Upper Silurian (Ludlow, lower Ludfordian), Rauchkofel Süd section, Carnic Alps, Austria; A, B, PMU 31743, A, lateral view showing the expanding adult shell, B, oblique lateral view; C, PMU 31744, lateral view showing the shorter initial shell; D, PMU 31745, lateral view. **E–H**, PMU 31746; E, lateral view of the most complete specimen showing initial and adult shell; F, dorso-apertural view; G, apertural view; H, enlarged apertural view to show recrystallized shell layer; **I**, PMU 31747, specimen with the broken initial part showing the depression left on the initial part of the adult shell.

SYSTEMATIC PALAEONTOLOGY

Genus *Jinonicella* Pokorný, 1978

Jinonicella kolebabai Pokorný, 1978
Figure 2A–I

1978a *Jinonicella kolebabai*, Pokorný, p. 39, figs 1, 2.
1978b *Jinonicella*, Pokorný, fig. 1.
1986 *Jinonicella kolebabai*, Hynda, pp. 48, 49, fig. 14, pl. 8, figs 1–4.
1994b *Jinonicella kolebabai*, Dzik, fig. 13E.
1999 *Jinonicella kolebabai*, Frýda, p. 27, figs 1, 2.
2006 *Jinonicella kolebabai*, Peel & Jeppsson, pp. 41, 42, fig. 1.
2006 *Jinonicella kolebabai*, Peel, pp. 1360, 1361, text-fig. 3.
2016 *Jinonicella kolebabi*, Chamberlain et al., pp. 25, 26, fig. 13K, L.
2017 *Jinonicella kolebabai*, Gubanov et al., pp. 216, 217, fig. 2.

Material. 11 pyritized specimens (PMU 31743–31753).

Description. The bilaterally symmetrical shell is minute, U-shaped, with a tubular snorkel protruding from the outer surface of the shell bend. The juvenile initial part of the shell with bulbous protoconch is straight or slightly curved before curving 180 degrees. It is about 350 to 450 µm long. A tube-shaped, circular siphon forms on the outer dorsal margin of the initial shell after it has revolved about 90 degrees. The teleoconch (adult shell) is a dorsally slightly compressed tube with a low rate of expansion. The teleoconch overlaps slightly the initial part of the shell so that a clear posterior depression on the adult shell is formed where it is in contact with the initial part.

STRATIGRAPHIC AND PALAEOGEOGRAPHIC DISTRIBUTION OF *JINONICELLA*

The oldest known *J. kolebabai* from the Middle Ordovician (middle Darriwillian) of Ukraine and Belarus of the Russian Platform (Hynda 1986) may not be conspecific with the holotype material (Frýda 1999), although the abundant (about 200 specimens), well-preserved shells show no discernible morphological differences from Silurian and Devonian specimens, including the holotype. Two occurrences of *Jinonicella* were later reported from the Late Ordovician of Poland (Dzik 1994a, 1994b). Eleven specimens identified as *Jinonicella* sp. n. by Dzik (1994b) were found in the Sandbian strata of the Lesieniec 1 borehole in north-eastern Poland, which penetrated the western margin of the Russian Platform (Modliński & Szymański 1997). Seven incomplete specimens, described as *Jinonicella* sp. (Dzik 1994a), were from the Katian part of the Mójcza Limestone of the Holy Cross Mountains of southern Poland.

In the Silurian *J. kolebabai* is known from the late Telychian of Utah, USA (Gubanov et al. 2017), the middle Sheinwoodian of Gotland, Sweden (Peel & Jeppsson 2006), the Ludfordian of Bohemia, Czech Republic (Pokorný 1978a) and the Carnic Alps (Dzik 1994b) of Austria. Devonian finds are reported from the Eifelian of Bohemia (Budil 1995) and the Givetian of Pennsylvania, USA (Chamberlain et al. 2016). The youngest representative of *Jinonicella* has been reported from the late Famennian strata of western Germany (Piecha 2004).

The unprecedented range of ca 80 million years (from the Middle Ordovician to the Late Devonian) for the species is remarkable and raises the question of whether there is a single species or an evolutionary sequence of alternating species. Unfortunately, at the moment the limited number of specimens, poor preservation and a very simple morphology, expressed by a restricted number of features, prevent further phylogenetic investigation.

The geographic distribution of *Jinonicella* is limited to Laurentia, Baltica and the European terranes of Bohemia, the Carnic Alps and the Holy Cross Mountains. The Mójcza Limestone of the Holy Cross Mountains is developed on the so-called Małopolska block which was part of Baltica since the Middle Cambrian (Walczak & Belka 2017). The unit has yielded trilobites and brachiopods of the Baltic affinities (Cocks 2002). In contrast, according to the majority of palaeogeographic reconstructions (e.g. Schönlaub 1992; von Raumer & Stampfli 2008), Bohemia, the Ardennes-Rhenish Massif (part of Avalonia) and the Carnic Alps (part of the Galatian terrane) have formed a group of high-latitude terranes that detached from Gondwana in the Ordovician and moved towards the equator during the Silurian and Devonian. Similarly, Baltica drifted from its high-latitude position in the Ordovician to an equatorial position during the Silurian when it accreted with Laurentia (Cocks & Torsvik 2006).

It appears that *Jinonicella* emerged in the Middle Ordovician in Baltica, in a temperate to subtropical climate. During the Ordovician the distribution of *Jinonicella* was limited to the western margin of Baltica (Fig. 3). The shift of Baltica towards a tropical climate may have allowed *Jinonicella* to survive the global cooling event during the Ordovician–Silurian transition – the second largest mass extinction in Earth history (Sheehan 2001). During the Silurian *Jinonicella* shows a wide distribution in Laurentia, Baltica, Bohemia and Galatian (Carnic Alps). Laurentia and Baltica were in an equatorial position (e.g. von Raumer & Stampfli 2008; Torsvik et al. 2014), while Bohemia and Galatian were close to the northern margin of Gondwana, i.e. in a mid-latitude climatic zone far from Laurentia/Baltica. It is unclear whether *Jinonicella* was dispersed to these remote terranes by palaeocurrents after the Ordovician–Silurian mass extinction event or if it was already present there in the Ordovician, but not discovered yet. Both scenarios are unlikely due to a low dispersal rate expected for a minute benthic or infaunal organism and the problems faced in crossing a wide, deep oceanic basin as well as surviving the end-Ordovician cooling in a high-latitude climatic zone. We should rather expect the presence of *Jinonicella* in Siberia, Kazakhstan, China and probably Australia, which were in the same climatic zone as Laurentia and Baltica. Ebbestad & Gutiérrez-Marco (2017) described the gastropod *Pterotheca* from the Silurian of Spain and noted the same unexpected distribution in a high-latitude peri-Gondwana area of a genus otherwise distributed exclusively in equatorial realms during the Ordovician and Silurian.

The tube-like, uncoiled protoconch in *Jinonicella* may be broadly compared with the uncoiled plankto-trophic embryonic shells of certain gastropods (see for instance Nützel 2014). Possible planktotrophy in *Jinonicella* could explain the Silurian distribution by adaptive radiation. In this case Bohemia and Galatian should already be close to Baltica and Laurentia in the Late Ordovician and Silurian. A wide distribution of the 'Bohemian-type' bivalve molluscs as well as the distribution of other benthic and pelagic fauna has been explained by the surface current circulation of the Silurian oceans (e.g. Kříž 1996; Bogolepova et al. 2005), but although a wide dispersal is possible for pelagic

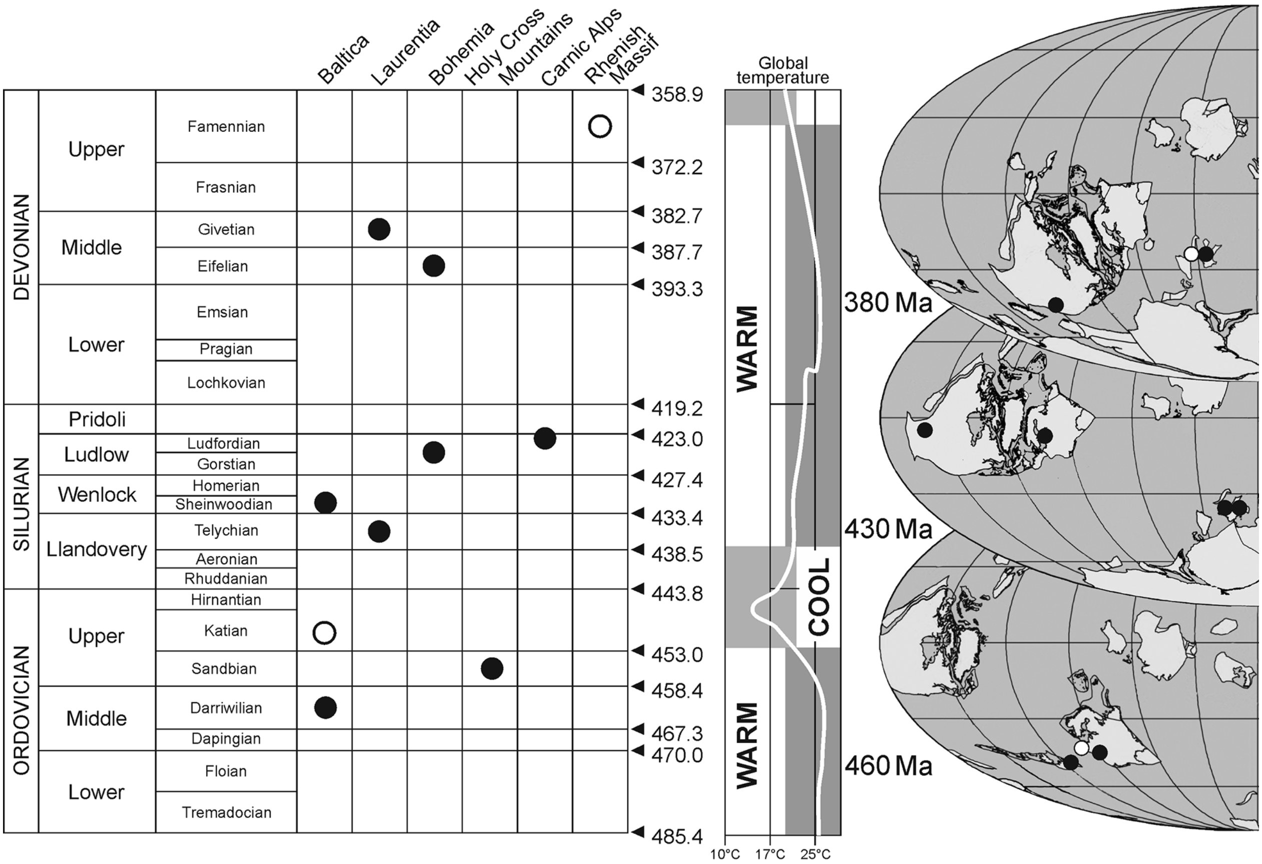

Fig. 3. Stratigraphic and palaeogeographic distribution of *Jinonicella kolebabai* (black circle) and *Jinonicella* sp. (white circle). Palaeogeography is after Torsvik et al. (2014), global temperatures adapted from Paleomap Project (http://www.scotese.com/climate.htm).

organisms such as cephalopods (Bogolepova 1995) and probably myodocope ostracods (Siveter & Bogolepova 2006; Perrier et al. 2014), the large number of various benthic organisms distributed from equatorial to polar areas is more difficult to explain with this model and the present palaeogeographical reconstructions.

During the Devonian, characterized by a warmer climate (Fig. 3), the distribution of *Jinonicella* is consistent with the existing palaeogeographic reconstructions.

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Mõistatusliku molluski *Jinonicella* uus leid Karni Alpide (Austria) Silurist

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Väike mõistatuslik mollusk *Jinonicella kolebabai* Pokorný, 1978 on kirjeldatud Cardiola kihistust (Ülem-Silur) Rauchkofel Südi paljandist Karni Alpides Austrias. Kaasnevad konodondid määravad leiu vanuseks Hilis-Ludlow' (Ludfordi) *Polygnathoides siluricus*'e tsooni. *Jinonicella* varasemad leiud Silurist on teada Wenlocki ja Ludlow' kivimitest Tšehhi Vabariigis, USA-s, Gotlandil (Rootsi) ning Karni Alpides Austrias. Selle taksoni laialdane levik Siluri eri kliimavööndites ja kaugetes üksteisest eraldatud aladel on küsimusi tekitav ning on ebaselge, kas *Jinonicella* oli esindatud kõrgete laiuskraadide aladel enne Ordoviitsiumi lõpul olnud jahenemise ja massilise väljasuremise perioodi või levis laiale alale Siluri jooksul. Ilmselt võiksid *Jinonicella* planktotroofia ja Siluri ookeani hoovuste muster taksoni levikut selgitada, kuid olevate paleogeograafiliste rekonstruktsioonide piires ei seleta see mudel adekvaatselt selle liigiga kaasnevate põhjafaunade levikut ekvaatorist kuni polaaraladeni.