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# An updated look at the taxonomy, stratigraphy, and palaeoecology of the Devonian bivalve genus *Ontaria* Clarke, 1904 (Cardiolidae, Bivalvia)

Judith Nagel-Myers[1]

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## Abstract

The genus *Ontaria* Clarke, 1904 includes a group of small, almost circular bivalves that occur abundantly in the Mid- and Late Devonian pelagic facies. These bivalves are characterised by their straight hinge line, small and, central beak, as well as commarginal rugae (if present). Based on an extensive review of type material and additional samples as well as a comprehensive literature review, this study identifies three valid species *Ontaria suborbicularis* Hall, *Ontaria concentrica* von Buch, and *Ontaria iniquistriata* Beushausen. Thirteen *Ontaria* species are either not valid or have been synonymised, and three species that were previously included in *Ontaria* do not belong to this genus. Representatives of *Ontaria* first occur in the late Eifelian and become abundant in the Frasnian and Famennian. *Ontaria* last occurs in the late Famennian before the Devonian/Carboniferous boundary. This genus has been identified as a representative of the family Cardiolidae previously reported only from the Silurian, making *Ontaria* the first report of a Devonian cardiolid taxon. *Ontaria* inhabited low-energy, generally well-oxygenated, off-shore environments. The overall shell morphology, small size, and the presence of a small siphon supports the idea that *Ontaria* lived semi-infaunal in/on muddy substrates.

**Keywords** Bivalves · Taxonomy · Stratigraphy · Palaeozoic · Devonian · *Ontaria* · Cardiolidae

## Introduction

Bivalves are commonly found in the deeper water faunas of the Mid- and Late Devonian and the fine-grained, siliciclastic sedimentary rocks and limestones deposited on the outer shelf preserve a low diverse invertebrate fauna (e.g. Wendt and Aigner 1985) frequently including bivalves (e.g. Becker 1993a; Kaever et al. 1980; Paeckelmann 1979). Unfortunately, these taxa have been largely overlooked because of poor preservation and an associated lack of taxonomic, stratigraphic, and palaeoecological data for these groups and the genus *Ontaria* Clarke, 1904 is no exception.

*Ontaria* is a small, almost circular bivalve with a straight hinge line developing characteristic strong commarginal ornamentation. These bivalves are easily identifiable and occur abundantly, sometimes covering bedding planes. *Ontaria* has been reported from the Middle and Upper Devonian of Germany (e.g. Becker 1993a), France (Babin 1966), Morocco (Nagel 2006), the Ural mountains (e.g. Kondiain et al. 1967; Tsinkoburova 2015), Western Australia (Teichert 1943), and North America (e.g. Cooper 1967; Kirchgasser 1983).

The re-examination of most of the type material from Germany and North America results in three valid *Ontaria* species and fourteen taxa identified as synonyms, many of which were described over a century ago based on a single or partial specimens (Table 1). This study outlines the stratigraphic range of *Ontaria* as far as currently known and offers a first palaeoecological interpretation of their presumed life habit.

*Ontaria* has often been confused with the Frasnian taxon *Paracyclas* Hall, 1843. *Paracyclas* is comprised of small, somewhat circular bivalves that develop strong commarginal ornamentation. But in *Paracyclas*, the posterior dorsal margin is curved and transitions smoothly into the posterior shell margin (e.g. LaRocque 1950) while *Ontaria*'s dorsal margin is straight and abruptly angles down into the posterior margin. *Paracyclas* umbo is prosogyrate and located in front of the centre of the

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✉ Judith Nagel-Myers
jnagel@stlawu.edu

[1] Geology Department, St. Lawrence University, 23 Romoda Drive, Canton, NY 13617, USA

**Table 1** Overview over *Ontaria* species and their synonyms (nomina dubia and nomina nuda included)

| | *O. concentrica* | *O. suborbicularis* | *O. iniquistriata* | Not ontariids |
|---|---|---|---|---|
| Synonyms | *Orbicula pectunculoides* | *Cardiola bisignata* | *Ontaria affiliata* | *Ontaria centurio* |
| | | *Cardiola clymenia* | *Ontaria tschernyschewi* | *Cardiola costatula* |
| | | *Ontaria pontiaca* | *Ontaria halli* | *Ontaria elegans* |
| | | *Ontaria accincta* | *Cardiola subarticulata* | |
| | | *Edmondia ? tenuistriata* | *Cardiola clarkei* | |
| | | | *Cardiola articulata* | |
| | | | *Cardiola infirma* | |

hinge line. *Ontaria* develops an orthogyrate to only slightly prosogyrate umbo that is centrally located. *Paracyclas* has been interpreted to be related to lucinids, and this study has found no evidence that suggests a relationship between *Paracyclas* and *Ontaria* (for revision of *Paracyclas*, see LaRocque 1950; Bailey 1983; Pojeta et al. 1986).

Originally, *Ontaria* taxa were included, together with many other small, somewhat circular bivalve taxa, in the Silurian genus *Cardiola* sensu Broderip (in Murchison 1839) until Clarke (1904) erected the genus *Ontaria* for these Devonian species. *Ontaria* is herein assigned to the family Cardiolidae (Cardioloidea, Praecardiidina; Carter et al. 2011), which were reported to disappear at the end of the Silurian (Kříž 1979, 2007), making *Ontaria* the only Devonian representative of this family (see phylogenetic remarks below). In the following systematic revision, taxonomic abbreviations based on Granzow (2000) are used (Table 2).

## Systematics

Suborder Praecardiidina Newell, 1965
Superfamily Cardioloidea R. Hoernes, 1884
Family Cardiolidae R. Hoernes, 1884

Genus *Ontaria* Clarke, 1904

**Type species:** *Ungulina suborbicularia* Hall, 1843 (SD Newell and LaRocque, 1969).
**Included species:** *Ontaria suborbicularis* Hall, *Ontaria concentrica* von Buch, *Ontaria iniquistriata* Beushausen.
**Diagnosis:** Valves small, subcircular to transverse oval, equilateral to slightly inequilateral. Umbo small, central, projecting little over hinge line, orthogyrate to slightly prosogyrate. Hinge line straight often ending posteriorly and anteriorly in three to six small radial ribs. Ornamentation can comprise a combination of strong, sometimes irregular, commarginal rugae, fine commarginal growth lines, and fine radial ribs. Dimyarian, with an oval posterior adductor scar that is larger than the irregularly shaped anterior scar. Pallial line developing a slight pallial sinus.

**Discussion:** Clarke (1904) described *Ontaria* based on specimens from the Frasnian of western New York State, thus, separating them from the upper Silurian genus *Cardiola* Broderip. *Cardiola* served as an umbrella taxon for many different somewhat circular Palaeozoic species and lacked a proper definition. Beushausen (1895) hesitantly assigned some Late Devonian taxa to *Cardiola* due to what he considered were transitional morphologies between *Cardiola* and the Late Devonian bivalve taxa.

Kříž (1979) re-studied the genus *Cardiola* and defined it as oval to subcircular in outline, with a prosogyrate umbo, markedly projecting above the hinge line. The ornamentation, which consists of strong radial ribs and distinct commarginal growth rugae, is particularly characteristic for this group. The radial and commarginal sculptural elements markedly intersect, giving the shell surface a "beehive-like" appearance (Kříž 1979). *Cardiola*'s ornamentation features characteristic growth bands, which divide the shell commarginally into several portions representing growth stages (Kříž 1979).

*Ontaria* develops a minute central umbo and lacks the typical ornamentation of *Cardiola*. This identifies them as distinct genera, but the observed similarities between some cardiolid taxa and *Ontaria* include both in the family Cardiolidae (see phylogenetic remarks below).

In the past, some taxa were erroneously included in *Ontaria*. Schmidt (1924) erected a new species from the Hangenberg beds of the northeastern Rhenish Massif, *Ontaria centurio* Schmidt. In the same study, he re-assigned *Cardium costatulum* Münster from the same stratigraphic level and localities to *Ontaria*. The examination of the two syntypes MB.M.21051 and MB.M.21052 (Fig. 1l–m) of *O. centurio* shows that these specimens are representatives of *Elasmatium elongata* Münster and not an *Ontaria* species (Nagel-Myers et al. 2009). He identified MB.M.21053 as *O. costatula* Münster (Fig. 1n), but, according to the revised taxonomy, this specimen is a lunulacardiid (sensu Nagel-Myers and Amler 2007). Schmidt's hypotypes include a specimen designated as *Ontaria aequilateralis* Schindewolf. This species was not part of his publication (1924), and, to my knowledge, it has not been published by Schindewolf or

any other author making it a nomen nudum. Examining the specimen shows that it is not a representative of *Ontaria*, but based on its fine radial ribs and its truncated posterior margin may be re-assigned to *Chaenocardiola*.

Zamjatin (1911, pl. 2, fig. 13) described *Ontaria elegans* from the Ural Mountains as developing a slightly inequivalve, strongly inflated shell with a prominent umbo that project far above the hinge line. Based on this description and his figure, this material cannot be included in *Ontaria*. The large beak and the inequivalve development of the shell make this species different from *Ontaria*. Unfortunately, it is difficult to systematically place this taxon with certainty without studying the types or associated material.

*Ontaria suborbicularis* (Hall, 1843)
(Fig. 1 g–i, k; Fig. 2c, e, f; Fig. 3c)

* +1843 *Ungulina suborbicularia* Hall, p. 243, fig. 106.2.
1883 *Cardiomorpha suborbicularis* Hall, pl. 63, figs. 9-10.
+1885 *Edmondia* ? *tenuistriata* Hall, p. 393, pl. 63, figs. 9-10.
nom. dub. 1895 *Cardiola bisignata* Beushausen, p. 350, pl. 37, fig. 6.
nom. dub. 1895 *Cardiola clymenia* Beushausen, p. 357, pl. 37, fig. 21.
1904 *Ontaria suborbicularis* Clarke, p. 282, pl. 8, figs. 1-20.
1904 *Ontaria suborbicularis* Clarke and Luther, p. 59, 60, 61.
+ 1904 *Ontaria pontiaca* Clarke, p. 287, pl. 8, fig. 21.
+ 1904 *Ontaria accincta* Clarke, p. 268, pl. 8, figs. 22-25.
1906 *Ontaria accincta* Kindle, p. 633.
1911 *Ontaria suborbicularis* Kindle, p. 348.
1911 *Ontaria suborbicularis* Luther, p. 18.
1911 *Ontaria suborbicularis* Zamjatin, pl. 2, figs. 5-7.
1911 *Ontaria* cf. *clarkei* Zamjatin, pl. 2, fig. 10.
1911 *Ontaria concentrica* Zamjatin, pl. 2, figs. 8-9.
1914 *Ontaria suborbicularis* Luther, p. 28.
1914 *Ontaria accincta* Luther, p. 25.
1914 *Ontaria pontiaca* Houghton, p. 89.
1935 *Ontaria pontiaca* Chadwick, p. 320.
1935 *Ontaria suborbicularis* Chadwick, p. 311, 321.
1935 *Ontaria accincta* Chadwick, p. 314.
1983 *Ontaria suborbicularis* Kirchgasser, p. 12, 23.
1994 *Ontaria accincta* Linsley, pl. 146, figs. 17-20.
1994 *Ontaria suborbicularis* Linsley, pl. 146, figs. 1-15.
2015 *Ontaria suborbicularis* Tsinkoburova, p. 41.

**Neotype** (designated herein): NYSM 5434 (Fig. 2e).
**Type locality:** Naples, Ontario Co., New York State, USA (42° 36′ 58″ N, 77° 24′ 9″ W)
**Type stratum:** "Naples beds," Sonyea Group, middle Frasnian, (UD I-D/F; Fig. 4).
**Diagnosis** (after Clarke 1904): Shell suborbicular in outline, somewhat inflated. Umbo is central and minute. Apical part of the umbo sometimes set off by a low transverse thickening, delineating the prodissoconch from the adult shell. Hinge line straight; area narrow, elongated, triangular, not elevated. Ornamentation consisting of fine commarginal growth lines, becoming more closely spaced towards the ventral margin; sometimes stronger rugae far apart developed, also covered by the fine ornamentation. When well preserved faint radial lines observable.
**Description:** Valves subcircular to transversely oval in outline, equilateral to slightly inequilateral, juvenile shell always subcircular, somewhat inflated. Dorsal margin straight, turning abruptly into convex anterior and posterior margin, both regularly merging into subcircular ventral margin (Fig. 1g, k). Umbo small, central, orthogyrate to slightly prosogyrate, hinge line straight (Fig.1 k).

Ornamentation consisting of fine commarginal growth lines, faint fine radial striae on the inside of the valve, and sometimes a few, widely spaced commarginal rugae. When present, strong commarginal rugae irregularly spaced, usually more prominent and closer spaced towards ventral margin, the prodissoconch often delineated by a ruga (Fig. 1i); rugae can be observed on the interior shell surface. Few pronounced, marginal radial ribs developed at the anterior and posterior end of dorsal margin (Fig. 1g, k); often valves appear smooth only displaying commarginal growth lines (Fig. 1i). Adductor scars dimyarian, pallial line with small indentation posteriorly; anterior adductor muscle smaller than posterior (Fig. 3c).

Neotype NYSM 5434 (Fig. 2e) presents the typical fine commarginal sculpture of this taxon and lacks any commarginal rugae. The hinge line is not fully visible, but the typical symmetric circular outline can be observed.
**Discussion:** Hall (1843) established *Ungulina suborbicularis* describing a shell from the middle Frasnian Sonyea Group. He (1883) figured a different poorly preserved specimen as *Cardiomorpha suborbicularis*, which he later (1885) re-described as *Edmondia* ? *tenuistriata*. Clarke (1904) re-studied the material and concluded that all these Hall specimens belong to *Ungulina suborbicularis.* Subsequently, Clarke (1904) re-assigned *U. suborbicularis* to his newly described genus *Ontaria*. Newell and LaRocque (1969) designated *U. suborbicularis* as type species of *Ontaria*. Most of Hall's type material is housed either in the American Museum of Natural History in New York or in the New York State Museum collections in Albany (Linsley 1994); the types could not be located in either location. This is not completely surprising since many of Hall's types are missing because he sold his fossil collections at least once in his career to raise money, and much of this material cannot be traced (Dott 2006). Since *Ungulina suborbicularis* is the type species of *Ontaria* and is widely used, NYSM 5434 (Fig. 2e) is designated as the neotype to stabilise the taxonomic situation of *Ontaria*'s type species. The neotype is from the same New York State units as the original Hall type, and it is the only one in Clarke's type

series that preserved the characteristic commarginal ornamentation (Fig. 2e).

In Beushausen's extensive review of Devonian bivalves from the Rhenish Massif, he (1895) described several new *Cardiola* taxa closely related to *Ontaria*. The type material was deposited in the collection of the Königlich-Preußische Geologische Landesanstalt in Berlin, which is now part of the Museum für Naturkunde. Inquiries with the collection in Berlin and searches of the databases of the Bundesanstalt für Geowissenschaften und Rohstoffe have been unsuccessful in tracking down many of the Beushausen *Cardiola* types. Beushausen (1895) described *Cardiola bisignata* from the upper Frasnian of Enkeberg (northeastern Renish Massif) based on one shell piece. Beushausen distinguished this species from other taxa based on the distinct delineation of the prodissoconch from the rest of the valve. This study shows that this morphology is common in *Ontaria*, suggesting that *C. bisignata* is a synonym of *O. suborbicularis*, rather than a new taxon. Due to the missing type material, *C. bisignata* is a nomen dubium.

Beushausen (1895) furthermore described *Cardiola clymenia* from the upper Frasnian of Enkeberg (northeastern Renish Massif), a species he noted is closely related to *O. concentrica*. It develops a prosogyrate umbo, which is located slightly before the middle of the shell. The hinge line is straight, and its ornamentation is the same as in *O. suborbicularis*. Beushausen's description of this taxon does not offer any morphologies that would separate this species from *O. suborbicularis* but rather characterises this single, poorly preserved specimen as a variation of the species. The lack of type material makes *C. clymenia* a nomen dubium.

Clarke (1904) erected a new *Ontaria* species, *O. pontiaca*, based on one specimen from the middle Frasnian of the Sonyea Group of Naples (western New York State); NYSM 5420 is the holotype by monotypy (Fig. 2f). This taxon is described as a typical *Ontaria* but lacking any type of ornamentation. The holotype examination shows that it is a steinkern and, thus, no inference about the original fine sculptural elements of this specimen can be made. *Ontaria*'s rugae are not limited to the outer shell but can be observed on the shell's interior surface (Fig. 1a). This steinkern lacks any commarginal rugae on its surface. Thus, NYSM 5420 is designated *O.* aff. *suborbicularis*, due to the absence of commarginal rugae.

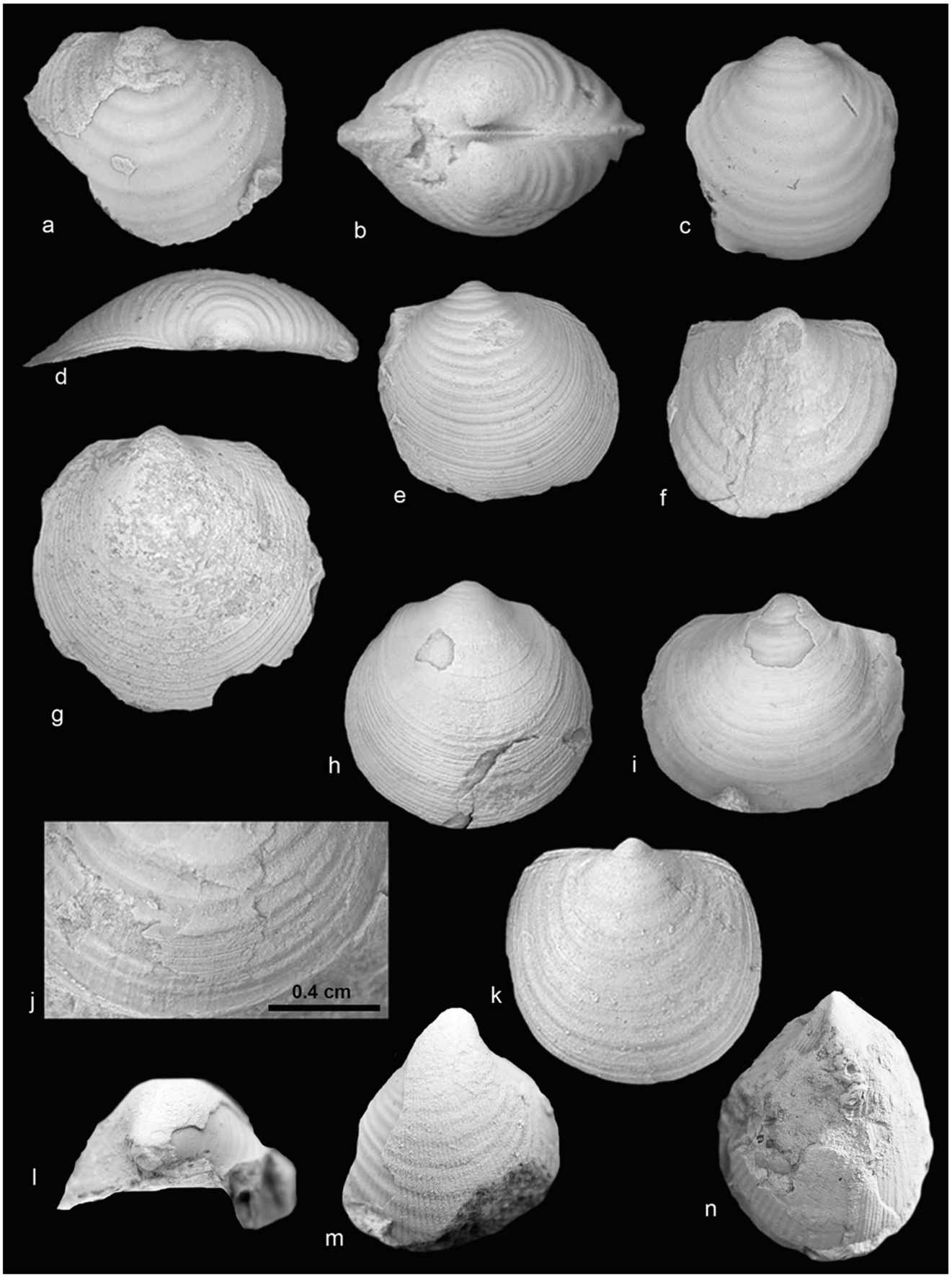
Another *Ontaria* species described by Clarke (1904) from Naples (western New York State) is *O. accincta*. The specimen NYSM 5402 from the middle Frasnian Sonyea Group is the holotype by monotypy. The holotype is a juvenile form of *O. suborbicularis*. The offset prodissoconch and its otherwise smooth shell and its small size and circular outline support this assumption. Clarke (1904) noted that this could easily be identified as *O. suborbicularis*, but interpreted this taxon as a more western variant of this taxon. As of now, there is no evidence supporting geographic variation in this group and, thus, *O. accincta* and *O. suborbicularis* are synonymised.

**Fig. 1** **a** *O. concentrica*, MB.M.2202.1 (lectotype *Orbicula concentrica*), LV, steinkern with shell remains, Martenberg, width: 1.13 cm; **b** *O. concentrica*, B6A-35.129, Oued Mzerreb, steinkern, width: 0.5 cm; **c** *O. concentrica*, MB.M. 259 (paralectotype *Cardiola subconcentrica*), Bad Wildungen, RV, steinkern, width: 0.6 cm; **d**, **e**, *O. concentrica*, MB.M. 2207.2, Oberscheld, RV, shell preservation, width: 1.6 cm; **f** *O. concentrica*, MB.M.4444.1, Oberscheld, RV, composite mold, width: 0.88 cm; **g** *O. suborbicularis*, B6A-35.131, Berigorn Valley Canning Basin, RV, shell preservation, width: 1.5 cm; **h** *O. suborbicularis*, MB.M. 2204, Oberscheld, LV, shell preservation, width: 1.24 cm; **i** *O. suborbicularis*, MB.M.4427, Oberscheld, LV, shell preservation, width: 1.36 cm; **j** *O. concentrica*, MB.M.4444.2, Oberscheld, ornamentation detail; **k** *O. suborbicularis*, MB.M.4435, Oberscheld, LV, shell preservation, width: 1.14 cm; **l**, **m** *O. centurio*, MB.M.21052 (syntype of *O. centurio*), Hönnetal, shell preservation, LV, width: 1.1 cm; **n** *O. costatula*, MB.M.21053, Hangenberg (hypotype Schmidt, 1924), shell preservation, RV, width: 1.4 cm. RV (right valve); LH (left valve)

**Occurrence:** Frasnian to middle Famennian (Fig. 4, supplemental Tables 3 and 4); Rhenish Massif, North America, Ural Mountains, Poland, France, Australia (supplemental Tables 3 and 4).

*Ontaria concentrica* (von Buch, 1832)
(Fig. 1a–f, j; Fig. 3a, b)

* + v1832 *Orbicula concentrica* von Buch, p. 50.
1842 *Cardium pectunculoides* d'Archiac and de Verneuil, p. 375, pl. 36, fig. 12.
non! 1843 *Cardiola concentrica* Roemer, p. 24, pl. 6, fig. 2.
1846 *Cardiola concentrica* Keyserling, p. 253.
+ 1850 *Cardium penctunculoides* Roemer, p. 26, pl. 4, fig. 10.
1856 *Cardiola concentrica* Sandberger and Sandberger, p. 273, pl. 29, fig. 1-1.
1882 *Cardiola concentrica* Holzapfel, p. 254.
1893 *Cardiola* sp. aff. *concentrica* Denckmann, p. 13, 15.
1893 *Cardiola concentrica* Denckmann, p. 15.
+ v 1895 *Cardiola subconcentrica* Holzapfel, p. 228.
non! *Edmondia tenuistriata* Hall 1885, p. 63, fig. 9.
1895 *Cardiola subconcentrica* Beushausen, p. 353, pl. 37, figs. 13-15.
1895 *Cardiola concentrica* Beushausen, p. 355, pl. 37, figs. 16-20.
1900 *Cardiola* aff. *concentrica* Beushausen, p. 165.
1901 *Cardiola concentrica* Denckmann, p. 35, 40.
1904 *Ontaria concentrica* Clarke, p. 286, pl. 8, fig. 26.
1908 *Cardiola subconcentrica* Torley, p. 41.
1911 *Ontaria articulata* Zamjatin, pl. 2, figs. 14-17.
1913 *Ontaria* aff. *arciformis* Paeckelmann, p. 256.
1914 *Ontaria concentrica* Houghton, p. 89.
1922a *Chaenocardiola concentrica* Henke and Schmidt, p. 35.
1922b *Cardiola subconcentrica* Henke and Schmidt, p. 21.
1924 *Ontaria concentrica* Paeckelmann, p. 58.
1931 *Cardiola concentrica* Matern, p. 124.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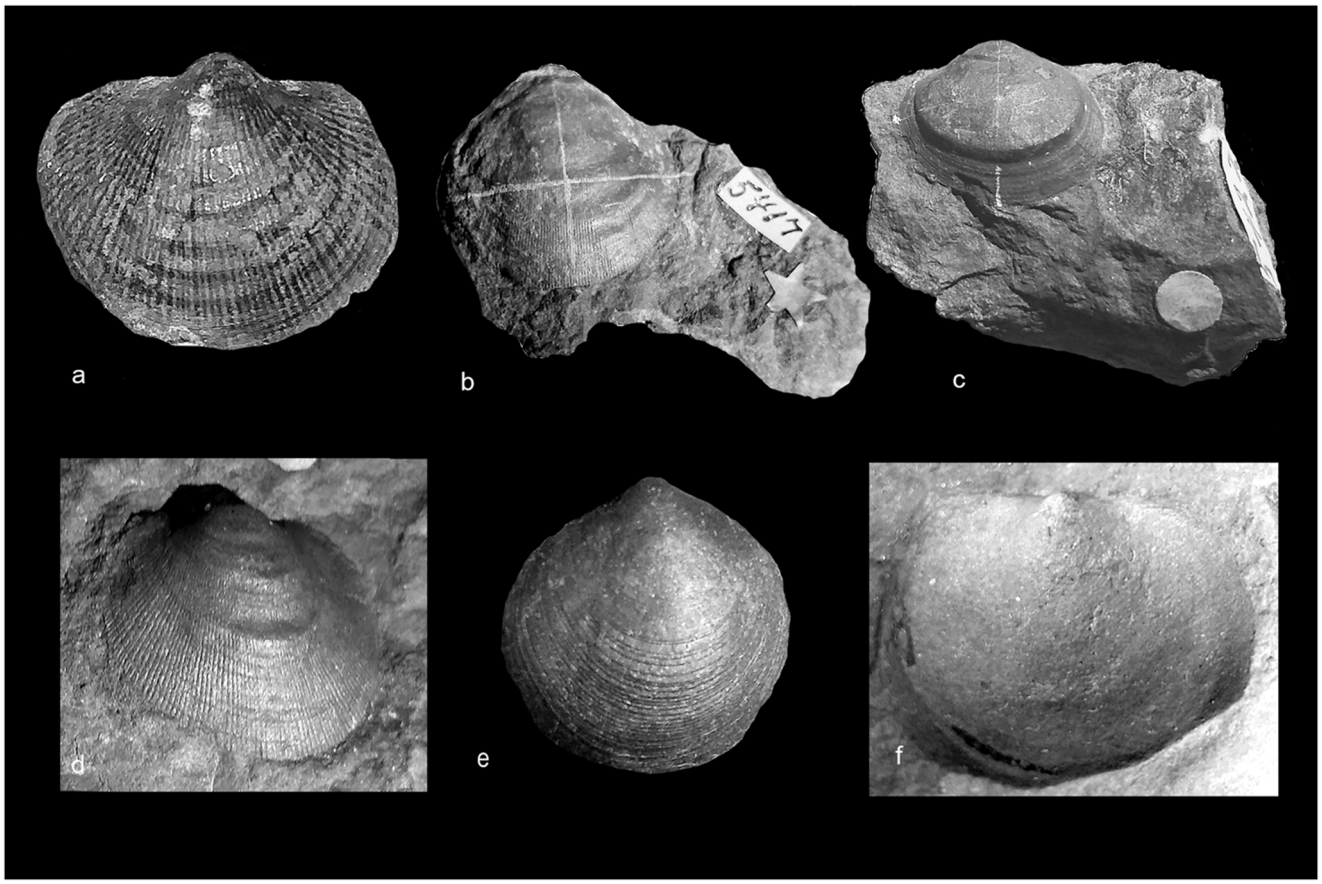


**Fig. 2** **a** *O. iniquistriata*, MB.M.257 (holotype *Cardiola iniquistriata*), Oberscheld, Rhenish Massif, external mold, width: 2.7 cm; **b** *O. iniquistriata*, NYSM 5417 (syntype *O. halli*), Naples, NY, composite mold, width: 2.8 cm; **c** *O. suborbicularis*, NYSM 5422, Naples, NY, internal mold, width: 1.5 cm; **d** *O. iniquistriata*, NYSM 5412 (*O. clarkei*), Naples, NY, composite mold, width: 1.8 cm; **e** *O. suborbicularis*, neotype, NYSM 5434, Naples, NY, composite mold, width: 1.86 cm; **f** *O. suborbicularis*, NYSM 5420 (holotype *O. pontiaca*), Naples, NY, internal mold, width: 3.7 cm

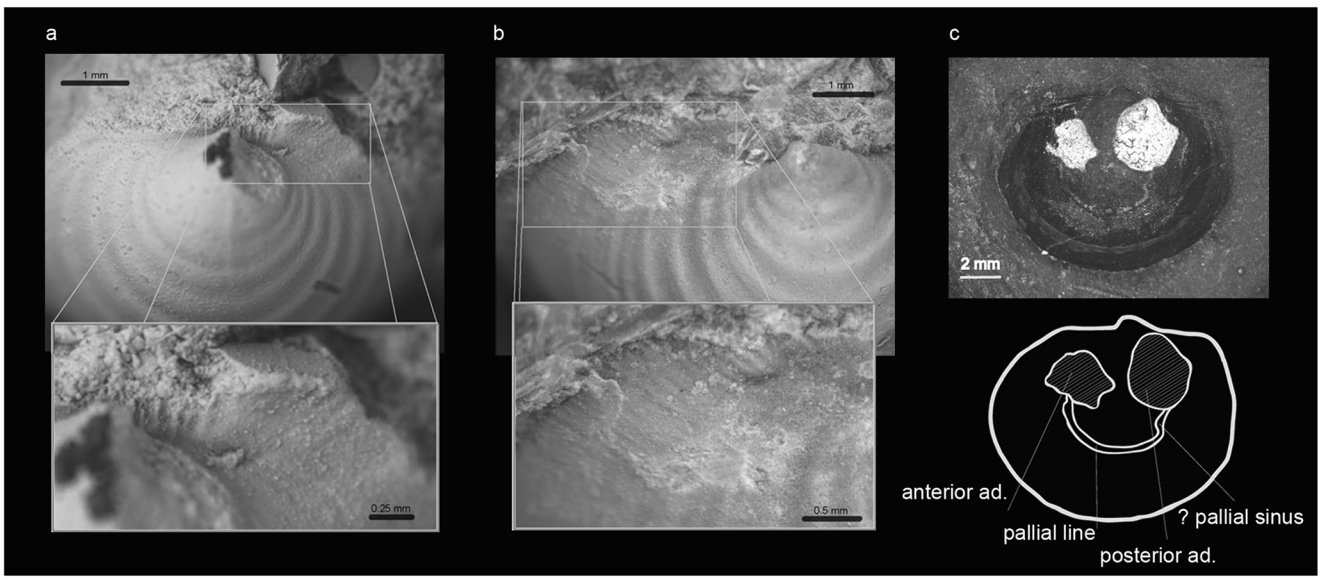


**Fig. 3** **a** Hinge development of *O. concentrica*; crenulation of the hinge area and dorsal margin (MB.M.259); **b** hinge development of *O. concentrica*, transition of fine radial ornamentation from ventral to dorsal margin (MB.M.258); **c** internal mold of *O. suborbicularis* showing phosphatised soft tissue structures (MB.M.4491)

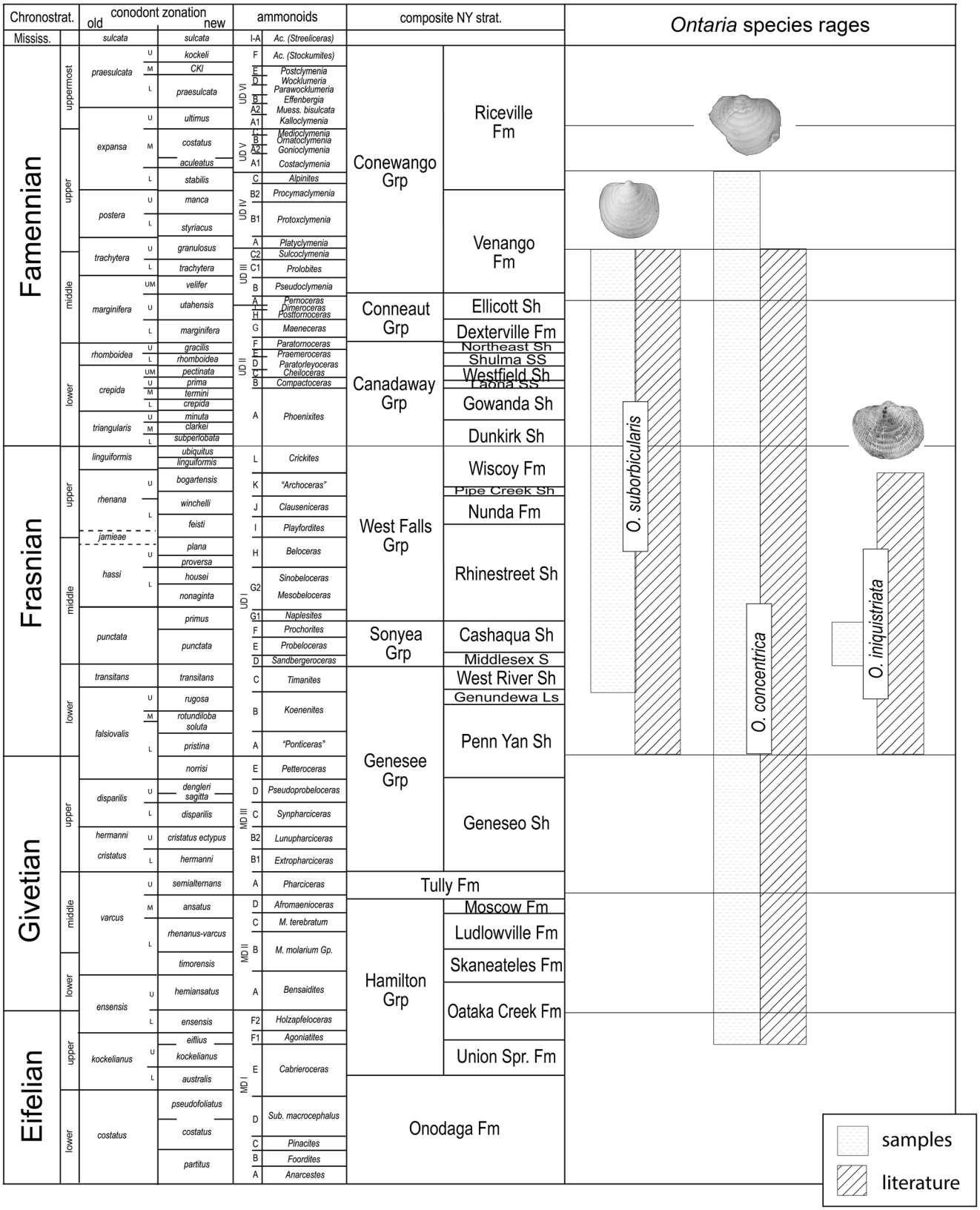


**Fig. 4** Stratigraphy of the examined material and range of *Ontaria* species based on examined material and literature mentions (after House 2002; Ver Straeten 2010; Königshof et al. 2016)

1935 *Ontaria concentrica* Chadwick, p. 324.
1936 *Cardiola concentrica* Paeckelmann and Kühne, p. 22, 23.
1965 *Cardiola concentrica* Bottke, p. 115, 124.
1966 *Ontaria subconcentrica* Babin, p. 118, pl.3, fig. 16.
1968 *Ontaria concentrica* Gunia, p. 183, pl. 10, fig. 23.
1979 *Cardiola subconcentrica* Paeckelmann, p. 24.
1979 *Cardiola concentrica* Paeckelmann, p. 19.
1980 *Cardiola concentrica* Kaever et al., p. 154, pl. 25, fig. 3.
1993b *Cardiola concentrica* Becker, p. 52, 78, 124.
1994 *Ontaria concentrica* Linsley, pl. 146, fig. 21.

**Lectotype** (designated herein): MB.M.2202.1 (Fig. 1a; preserved on a slab with several other bivalves).
**Type locality:** Martenberg, northern Hesse, Germany (51° 22′ 30.2″ N, 8° 48′ 46.4″ E).
**Type stratum:** "Adorf Kalk", upper Frasnian, (UD I-I/J; Fig. 4).
**Diagnosis (revised):** Valves subcircular to transverse in outline. Ornamentation consisting of strong, regularly, or irregularly spaced commarginal rugae and faint radial lines on inside of valve; additional fine, irregular, commarginal growth lines covering the whole shell. Towards the ventral margin, strong commarginal rugae become less frequent.
**Description:** Shell subcircular to transversely oval, equilateral to slightly inequilateral, valves somewhat more inflated than *O. suborbicularis*. Dorsal margin straight, anterior and posterior margin broadly convex regularly merging into subcircular ventral margin. Umbo small, central, orthogyrate to slightly prosogyrate. Prodissoconch sometimes delineated by one ruga (Fig. 1b). Hinge line straight, crenulated, generating interlocking indentations below the umbo (Fig. 3a, b).

Ornamentation consisting of strong commarginal growth rugae, predominant on the dorsal portion of the shell, disappearing towards the ventral margin (Fig. 1e). Shell covered by fine, irregular, commarginal growth lines, bundling towards the ventral margin (Fig. 1j). Fine radial lines irregularly spaced, when preserved well faintly observable on steinkern (Fig. 1j). Parallel to dorsal margin posteriorly and anteriorly short, marginal crenulation, intersecting with commarginal growth lines (Fig. 1f).

Lectotype MB.M.2202.1 (Fig. 1a) subcircular in outline, lacking ventral margin, hinge line, and apical portion of umbo. The main portion of the shell presenting smooth steinkern with faint radial lines. Posterodorsal portion of the valve presents shell remains with fine commarginal growth lines and two radial ribs parallel to the dorsal margin.
**Discussion:** Von Buch (1832) described the abundant occurrence of a subcircular bivalve from Martenberg (northeastern Rhenish Massif, Germany) and named them *Orbicula concentrica*, which he surprisingly assigned to a brachiopod genus. Subsequently, Keyserling (1846) re-assigned von Buch's species to *Cardiola*. Von Buch's types are preserved on one slab with several other bivalves. I designate one well-preserved specimen (MB.M.2202.1) as lectotype for this taxon (Fig. 1a).

Roemer (1850) described a new species from the Frasnian "Goniatitenkalk" of the Harz Mountains, Germany, *Cardium penctunculoides*. The figured specimen (1850, pl. 4, fig. 10) and the description identify it as *Ontaria* species with commarginal rugae, and it is, thus, a subjective synonym of *O. concentrica*. The material Roemer (1843) identified as *C. concentrica* from Iberg, Germany, is extremely inequilateral and not a representative of *Ontaria*.

Beushausen (1895) described a new species *C. subconcentrica* from the Kellwasser beds of Ense (Kellerwald, eastern Rhenish Massif, northern Hesse, Germany) and the Middle Devonian "Stringocephalenkalk" of Martenberg (northeastern Rhenish Massif, Germany). The types (MB.M.258-60, Fig. 1c) are material of the Denckmann collection from the Middle Devonian "Odershäuser Kalk" (Kellerwald, eastern Rhenish Massif, Germany).

The Denckmann collection was, among others, the basis of Beushausen's monograph (Beushausen 1895), and this material is, in all probability, the material Denckmann (1893) described as *Cardiola* sp. aff. *concentrica*. Beushausen (1895) described the development of the hinge line to be the only distinguishing feature of both species. He assumed *O. concentrica* to be edentulous, while *C. subconcentrica* develops interlocking indentations at the dorsal margin. His assumption that *O. concentrica* is edentulous could not be confirmed in the examined material, and re-examination of the type material and additional samples provides neither the chance to observe *C. subconcentrica*'s teeth nor confirmed the lack of area underneath the beak. Out of the types, MB.M.258 (Fig. 3b) is chosen as the lectotype of *Cardiola subconcentrica*. The lectotype and paralectotypes MB.M.259 (Fig. 3a) and MB.M.260 develop the characteristic commarginal ornamentation of *O. concentrica*, and, therefore, *Cardiola subconcentrica* is a junior synonym of the latter.

Paeckelmann (1913) identified material from the Upper Devonian of the Bergisches Land (northwestern Rhenish Massif, Germany) as *Ontaria* aff. *arciformis*. His description of an *Ontaria* valve with strong commarginal ornamentation lacking any radial sculpture identifies his samples as *O. concentrica*.
**Occurrence:** Uppermost Eifelian to lower Famennian (Fig. 4, supplemental Tables 3 and 4); Rhenish Massif, North America, Morocco (supplemental Tables 3 and 4).

*Ontaria iniquistriata* (Beushausen, 1895)
(Fig. 2a-b, d)

*1840 *Cardiola articulata* Münster, p. 69, pl. 9, fig. 2. (non fig. 1). [nom. dub.]

1882 *Cardiola articulata* Holzapfel, p. 254, pl. 48, figs. 9 a-c.
v + *1895 *Cardiola iniquistriata* Beushausen, p. 347, pl. 36, fig. 11.
* nom. dub. 1895 *Cardiola subarticulata* Beushausen, p. 335, pl. 37, figs. 4.5.
* nom. dub. 1895 *Cardiola infirma* Beushausen, p. 346, pl. 34, fig. 17.
* nom. dub. 1895 *Cardiola clarkei* Beushausen, p. 347, pl. 34, fig. 10.
v + *1904 *Ontaria clarkei* Clarke, p. 298, pl. 7, figs. 10-20.
v + *1904 *Ontaria affiliata* Clarke, p. 290, pl. 7, figs. 21, 22.
v + *1904 *Ontaria halli* Clarke, p. 290, pl.7, figs. 23-21, pl. 8, fig. 28.
1904 *Ontaria affiliata* Clarke and Luther, p. 61.
1904 *Ontaria halli* Clarke and Luther, p. 61.
1904 *Ontaria clarkei* Clarke and Luther, p. 61.
+ 1911 *Ontaria tschernyschewi* Zamjatin, p. 26, pl. 2, figs. 11, 12.
1913 *Ontaria subarticulata*, Paeckelmann, p. 255.
1914 *Ontaria clarkei* Luther, p. 28.
1919 *Ontaria clarkei* Kindle, p. 3, 5, pl. 1, fig. 8.
1930 *Ontaria halli* Raymond, p. 296.
1935 *Ontaria halli* Chadwick, p. 314.
1935 *Ontaria clarkei* Chadwick, p. 314.
1935 *Ontaria affiliata* Chadwick, p. 314.
1966 *Ontaria subradiata* Babin, p. 119.
1994 *Ontaria halli* Linsley, pl. 146, fig. 16.
1994 *Ontaria clarkei* Linsley, pl. 146, figs. 1-8.
2015 *Ontaria clarkei* Tsinkoburova, p. 38, 41.

**Holotype** (by monotypy): MB.M.257 (Fig. 2a).
**Type locality:** Oberscheld, Dillenburg, Hesse, Germany (50° 44′ 23.7″ N, 8° 21′ 28.8″ E)
**Type stratum:** "Goniatitenkalk," upper Frasnian (UD I-I/J, Fig. 4)
**Diagnosis (revised):** Valves subcircular to transverse in outline. Ornamentation consisting of 80 to 100 radial ribs, sometimes associated with a variable number of strong, irregularly spaced commarginal rugae and fine commarginal striae.
**Description:** Shell subcircular to transversely oval, equilateral to slightly inequilateral, valves slightly larger and somewhat more inflated than *O. suborbicularis* and *O. concentrica*.

Dorsal margin straight, anterior and posterior margin broadly convex regularly merging into subcircular ventral margin (Fig. 2a). Umbo slightly larger and more inflated than in other *Ontaria* taxa, central, slightly prosogyrate; prodissoconch sometimes offset from the rest of the shell.

Hinge and internal structures not observable in the material.

Ornamentation consisting of varying degrees of irregularly spaced strong commarginal growth rugae, predominant on the dorsal portion of the shell, disappearing towards the ventral margin, fine commarginal growth lines can be present (Fig. 2b, d). A variable number of fine, radial ribs cover the whole shell. This is the only *Ontaria* species that combined all the commarginal sculptural elements with radial ribs.

The holotype MB.M.257 (Fig. 2a) is a well-preserved specimen from the Sessacker Trench in town of Oberscheld (Lahn Dill Syncline, Germany) preserving the outer shell surface. It clearly shows the combination of rugae, fine commarginal ornamentation, and radial ribs characteristic for this taxon. The dorsal margin is straight, and the hinge is not preserved. The transition to the anterior and posterior margins develops slightly more defined radial ribs but not as accentuated as in other specimens.
**Discussion:** The taxonomic situation of this species is complicated. Representatives of this *Ontaria* taxon with radial ribs in addition to the commarginal ornamentation have been described under several different species names. Based on the principle of seniority, *Cardiola articulata* Münster would be the valid name for this species. Still, neither the type specimens nor any associated material of *C. articulata* could be found in the Bayerische Staatssammlung für Paläontologie und Geologie in München, where most of Münster's type material is deposited. Based on personal communication with Winfried Werner, the types of *Cardiola articulata* seem to be missing at least since before 1925, which is supported by the work of Holzapfel (1882), who already relied solely on Münster's figures to identify his material. Inquiries with the Museum für Naturkunde in Berlin and the collection database for the Bundesanstalt für Geowissenschaften und Rohstoffe (BGR) in Berlin were also unsuccessful in locating the type material. Thus, *Cardiola articulata* Münster is a nomen dubium.

Beushausen (1895) described *Cardiola iniquistriata*, *Cardiola infirma*, *Cardiola subarticulata*, and *Cardiola clarkei*, and based on his illustrations and description these taxa are all closely related to *Ontaria*. Unfortunately, except *Cardiola iniquistriata*, Beushausen's *Cardiola* type material could not be located. For this study, an extensive search of collection databases and communication with the collection

**Table 2** Abbreviations used in this study (Granzow 2000)

| | |
|---|---|
| + | New taxon |
| * | Original description |
| e.p. | Ex parte/partial |
| v | Vide, specimens of this reference have been re-studied |
| non | Does not belong to this taxon |
| nom. dub. | Nomen dubium |
| nom. nud. | Nomen nudum |
| SD | Subsequent designation |
| NYSM | New York State Museum, Albany |
| MB.M | Museum für Naturkunde, Berlin |
| B6A-35 | Westfälische Wilhelms Universität Münster |

managers of the Museum für Naturkunde, the BGR in Berlin, and the Bayerische Staatssammlung für Paläontologie und Geologie, have been unsuccessful in tracing the type material.

The only type found is specimen MB.M.257, *Cardiola iniquistriata,* from the Sessacker Trench in the town of Oberscheld (Lahn Dill Syncline, Germany); MB.M.257 is the holotype by monotypy.

*C. infirma*'s postlarval interruptions of shell development (Beushausen 1895) echo the morphologies of *Ontaria*, which develops similar changes in growth direction (e.g. Fig. 2c). This feature, combined with its ornamentation and overall morphology, as described by Beushausen, suggests that *C. infirma* is a representative of *O. iniquistriata*, but due to the lack of type material *C. infirma* is a nomen dubium.

Beushausen (1895) erected *Cardiola subarticulata* describing two specimens from Martenberg (northeastern Rhenish Massif, Germany). He described their close relationship to *C. articulata* and stated that it is most likely a local (Martenberg) variation of *C. articulata*. Subsequently, Paeckelmann (1913) placed *C. subarticulata* in the genus *Ontaria*. This taxon develops *Ontaria*'s typical radial and commarginal sculpture elements, and, thus, C. *subarticulata* is a representative of *O. iniquistriata*. Despite its likely taxonomic affiliation, *C. subarticulata* is a nomen dubium due to its missing types.

Beushausen described *Cardiola clarkei* from the upper Frasnian of Oberscheld (Lahn Dill Syncline, Germany). These types could not be located. But Clarke (1904) identified *O. clarkei* specimens based on the examination of Beushausen's original material. Thus, his hypotypes are the closest material to the original types of *O. clarkei* that could be located. Therefore, specimen NYSM 5412 is selected from Clarke's hypotypes as a neotype for *C. clarkei*. Based on the morphology of the neotype and original descriptions and figures of Beushausen (1895), *C. clarkei* is determined to be a junior synonym of *O. iniquistriata*.

Clarke (1904) erected two *Ontaria* species. *O. affiliata* is based on a single valve (NYSM 5404) from the Frasnian of western New York State; this specimen is the holotype by monotypy. Clarke (1904) states that this taxon is more convex than *O. iniquistriata* and develops finer radial ornamentation. The examination of the holotype offered no distinct difference to *O. iniquistriata*. The holotype develops approximately 93 radial ribs and is subcircular in outline with a straight hingeline which ends in a few strong marginal ribs at the end of both sides of the dorsal margin; its umbo is small, central, and slightly prosogyrate, and the degree of valve inflation is the same as that observed in *O. iniquistriata*. These features indicate that the holotype is representative of *O. iniquistriata*, making *O. affiliata* a junior synonym of *O. iniquistriata*.

Clarke (1904) described a new species, *O. halli*, from the Frasnian of Naples (western New York State) and noted its close affiliation to *C. subarticulata*, which is synonymised with *O. iniquistriata* herein (see above). He described this taxon as less convex but qualified his statement by adding it could be a variation of the latter. Examining the syntypes (NYSM 5417-19) shows that they are slightly compressed. Additionally, he noted the presence of fine commarginal striae that he describes as a typical feature of *O. halli*. This study's survey of material clearly shows that these fine commarginal lines are present in all well-preserved *Ontaria* specimens. Thus, *O. halli* is a junior synonym of *O. iniquistriata*.

Zamjatin (1911) described *O. tschernyschewi* from the Ural Mountains. He noted the similarities to German cardiolids and described the typical radial ornamentation combined with commarginal rugae. Zamjatin mentioned size to be one of the biggest differences to the already existing taxa. Unfortunately, the originals have not been examined in this study, but his figures place this species into *O. iniquistriata*. Thus, *O. tschernyschewi* is a junior subjective synonym of *O. iniquistriata*.

**Occurrence:** Frasnian (Fig. 4, supplemental Tables 3 and 4); Rhenish Massif, North America, Ural Mountains (supplemental Tables 3 and 4).

## Stratigraphic range

Palaeozoic bivalves are seldom used for biostratigraphical zonation. The lack of an updated taxonomy has often hindered comprehensive treatments of these taxa for stratigraphic purposes. The few studies using bivalves in the mid-Palaeozoic have shown that they can be a valuable addition to traditional biozonation (e.g. Amler 2004, 2014; Grimm 1998; Sadykov 1962). The compilation of data in this study is the first time *Ontaria*'s stratigraphic range has been outlined based on an updated taxonomy, literature review, and examined material.

The genus *Ontaria* first occurred in the late Eifelian (Fig. 4), and the genus became extinct in the Famennian (Fig. 4). In the past, the last occurrence of this taxon has been inaccurately identified as the earliest Mississippian of the Rhenish Massif (Germany). Schmidt (1924) misidentified two species as *Ontaria* and, subsequently, these taxa have erroneously extended the range of this group (e.g. Amler 1992, 2004; Becker 1988). The re-examination of Schmidt's type material for this study shows that these taxa are not representatives of *Ontaria*.

The longest ranging *Ontaria* species is *O. concentrica*; it first occurs in the late Eifelian of the Rhenish Massif. Both the examined material and the occurrences described in the literature have confirmed this (Fig. 4). The oldest material is from the black limestones of the uppermost upper Eifelian of the Kellerwald. *Ontaria concentrica* occurs abundantly throughout

the Frasnian, sometimes covering bedding planes. During the Famennian, *O. concentrica* occurs less frequently and disappears in the late Famennian (Fig. 4, supplemental Tables 3 and 4).

Clarke (1904) described *O. suborbicularis* from the Frasnian shales of the Sonyea Group in Yates, Ontario, Livingston, Genesee, and Erie counties, and contemporaneous units around Canandaigua Lake (central New York State). These records represent the first occurrences of this taxon in the Frasnian. Previously, this taxon has not been described from outside of North America. As this study shows, this does not indicate a lack of *O. suborbicularis* in the rest of the world, but rather the unfamiliarity of researchers outside the USA with this species. The last occurrence of the taxon is represented by specimens from the Rhenish Massif (Germany). Stratigraphic specifications associated with this material are limited to "Enkeberger Kalk," which can only broadly be interpreted as lower Famennian (UD II/III), and samples from the Beyrich collection representing this taxon are only labelled as "Upper Devonian" making a precise stratigraphic interpretation impossible. Therefore, the last occurrence of *O. suborbicularis* is conservatively designated as UD III.

The stratigraphic range of *Ontaria iniquistriata* is the shortest of this genus (Fig. 4). This taxon first occurs in the early Frasnian and, based on the material examined here, does not extend into the Famennian. But caution is advised regarding this stratigraphic distribution since most of the examined material for this taxon is from North America. Just as with *O. suborbicularis*, future work will probably reveal an extended spatial and temporal range of *O. iniquistriata*.

## Phylogenetic remarks

*Ontaria* belongs to a group of Palaeozoic bivalves that originated in the Silurian and became extinct sometime at the beginning of the Carboniferous. Unfortunately, due to their often poor preservation, not much data is available for this bivalve group. Consequently, higher taxonomic affiliation and phylogenetic relationships of these Palaeozoic bivalves are not well understood. Kříž (2007) revised the higher taxonomy of these bivalves and erected the superfamily Nepiomorpha Kříž 2007. In their synoptically summary of suprageneric classification of bivalves, Carter et al. (2011) synonymised Nepiomorpha with the suborder Praecardiinida Newell 1965. But Kříž's concept of these bivalves representing a "successful, almost 100 myr of evolutionary experiment (Silurian–Devonian)" which produced bivalves with peculiar features like peg-like or conical teeth forming a pseudotaxodont structure or characteristic commarginal growth bands delineating abrupt postlarval changes in shell growth remains well-founded. His work focused mainly on Silurian and Early Devonian material (for review Kříž 2007) and, thus, the relationship to Mid- and Late Devonian taxa remains largely unstudied (e.g. Hryniewicz et al. 2018).

In his original description of *Ontaria*, Clarke (1904) emphasised the relationship between this Devonian genus and the Silurian cardiolids, buchiolids, and praecardiids, all of which are all included in the suborder Praecardiinida. According to Kříž (2007), only the superfamily Praecardioidae includes Devonian representatives, and all Cardioloidea became extinct at the end of the Silurian. But the revision of *Ontaria* suggests that this Devonian genus shows more affinity to the family Cardiolidae than to the heavily radially ribbed, triangular-shaped taxa of the pracardiidae. Buchiolids resemble the circular outline of *Ontaria*, but the pronounced buchiolid radial ornamentation and the lack of *Ontaria*'s characteristic commarginal rugae place *Ontaria* closer to Cardiolidae than the Devonian Buchiolidae. This is further supported by the buchiolid pseudotaxodont hinge development, which differs from the edentulous *Ontaria*.

Kříž revised the cardiolids and their phylogeny (Kříž 1979, 2007). Based on his description of this family, *Ontaria* has many characteristic features in common with cardiolids, including a prosogyrate beak, characteristic growth interruptions, the general lack of true hinge teeth, and a reduced anterior adductor muscle. In 2005, Kříž described *Cardiva* as a new ancestral genus of the Cardiolidae. This early Silurian taxon is reminiscent of the Devonian *Ontaria*. *Cardiva* develops the same commarginal sculpture observed in *Ontaria*, which Kříž described as "developed as regularly or irregularly spaced wider growth bands of variable convexity, and as growth furrows." *Cardiva* lacks strong radial ribs but develops marginal crenulations, which resemble the dorsal margin development in *Ontaria*. These morphologies and the illustrated holotypes from the Silurian of Spain (Kříž 2005) strongly suggest a phylogenetic relationship between these two genera. Based on its commonalities with *Ontaria*, *Cardiva* is interpreted as the common ancestor of the Silurian cardiolid taxa and *Ontaria*.

The early Silurian *Cardiva* is distributed mainly on the carbonate shelfs of Peri-Gondwana margins (central-southern Europe) (Kříž 1979). During the Silurian, these taxa radiated and have settled in similar off-shore environments of, e.g. Baltica, Laurentia, Australia, and Siberia (Cope and Kříž 2013; Kříž 2007). Palaeogeographic reconstructions have shown that marine pathways between Gondwana and Laurussia were open during the Silurian and Devonian, explaining the faunal links between them (Bailey 1978; Golonka 2020). The common ancestor of the cardiolids and *Ontaria* suggests that the latter represents a branch of the Cardiolidae that has evolved separately from the late Silurian cardiolid population of the Peri-Gondwana in the new world, expanding their spatial distribution in the Mid- and Late Devonian. This is supported by the stratigraphic range of the *Ontaria* species. The commarginal sculpture that *Cardiva* and *Ontaria* have in common is most pronounced in *O. concentrica*, which is also the oldest *Ontaria* species. In the

younger species, the commarginal rugae become less pronounced and less frequent.

In sum, this study shows sufficient commonalities between the Cardiolidae and *Ontaria* to justify including *Ontaria* at least preliminarily in this family. I suggest that more data from Mid- and Late Devonian bivalve communities will clarify if the creation of a new family is needed or more Devonian cardiolid taxa will emerge.

## Palaeoecological interpretation

Although we have only little information about the life habits of *Ontaria*, based on shell morphology and soft body organisation, we have some indication on how these bivalves might have adapted to their environment.

The majority of the examined material is from off-shore deposits represented by either arenaceous shales and nodular limestones from the Appalachian foreland basin of central and western New York State (Kirchgasser 1983) or nodular limestones, cephalopod limestones, or argillaceous shales and siltstones from the Rhenish Massif (Germany) and vicinities (e.g. Becker 2008; Königshof et al. 2016).

These fine-grained sedimentary rocks have been deposited in generally well-oxygenated settings characterised by low sedimentation rates (e.g. Kaiser et al. 2011; Wendt and Aigner 1985). These units often accumulated on topographic highs like drowned reefs, volcanoes, or submarine swells (Kirchgasser 1983; Königshof et al. 2016). The water depth of these low-energy environments has been reconstructed as below the photic zone and fair-weather wave base, somewhere from 10 to 100 m (e.g. Bábek et al. 2018; Kaiser et al. 2011; Wendt and Aigner 1985)

The Silurian ancestral taxa have been reconstructed as semi-infaunal to epibyssate (e.g. Kříž 2005, 2007). Devonian buchiolids that develop valve morphologies similar to *Ontaria* lived in similar environments and have been interpreted as shallow infaunal organisms (Grimm 1998). The only evidence for the softbody organisation of *Ontaria* is provided by an internal mold of *O. suborbicularis* preserving phosphatised soft tissue structures, including a shallow pallial sinus (Fig. 3c). The development of a small siphon supports the idea that *Ontaria* was living partially sunk-in the muddy substrates they were inhabiting. The small siphon extended up out of the mud into the water column but was too short of supporting a fully infaunal lifestyle. The majority of shells are around 1 cm in size, and the largest individual only reaches around 2 cm. Small body size maximizes the organism's surface-volume ratio, providing more support of the substrate per unit of animal weight for these bivalves and preventing them from sinking in the mud too far (Stanley 1970).

The overall shell morphology and size, the small siphon, and lack of true hinge teeth support the idea that *Ontaria* lived sunk-in semi-infaunal in/on the muddy substrates. Some authors have speculated that similar bivalves found in these units may have been chemoautotrophic or mixotrophic (e.g. Grimm 1998), but no evidence for such adaptations has been observed in this material.

## Conclusion

This study of the Devonian genus *Ontaria* has, for the first time in over a century, updated the taxonomy of this bivalve group, compiled data on its stratigraphic range, outlined its phylogenetic relationships, and reconstructed a possible lifestyle for this genus.

- *Ontaria* is a small, dimyarian bivalve genus developing a reduced anterior adductor muscle and a small siphon. This taxon lacks true hinge teeth; instead, the dorsal margin is crenulated and develops a few strong radial ribs at the posterior and anterior end of the dorsal margin to enhance valve coherence. These bivalves' most characteristic feature is their subcircular outline, a small central umbo, and strong commarginal rugae.
- *Ontaria* includes three valid species, and this study identified thirteen synonymised species.
- The species are mainly distinguished based on differences in ornamentation. *O. concentrica* develops strong commarginal rugae, *O. suborbicularis* is almost smooth with few or no rugae, and *O. iniquistriata* is the only *Ontaria* species that develops fine radial ribs in additions to commarginal sculptural elements.
- *Ontaria* is the youngest representative of the family Cardiolidae. The Silurian cardiolid species *Cardiva* has been identified as the common ancestor of *Ontaria* and Silurian cardiolids, suggesting migration pathways between Gondwana and Laurussia during the Silurian.
- *Ontaria* first appears in the late Eifelian and last occurs in the Famennian; this genus can be found worldwide in the Middle and Upper Devonian pelagic sedimentary rocks.

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## Declarations

**Conflict of interest** The authors declares that they have no conflict of interest.

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