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Complete List of Authors:	Ferrari, Mariel; Instituto Patagónico de Geología y Paleontología (IPGP, CCT CONICET-CENPAT) Little, Crispin; University of Leeds, School of Earth and Environment Atkinson, Jed; University of Leeds, School of Earth and Environment
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LATE TOARCIAN (LOWER JURASSIC) MARINE GASTROPODS FROM THE CLEVELAND BASIN, ENGLAND: SYSTEMATICS, PALAEOBIOGEOGRAPHY AND CONTRIBUTION TO BIOTIC RECOVERY FROM THE EARLY TOARCIAN EXTINCTION EVENT

by MARIEL FERRARI,[1*], CRISPIN T.S. LITTLE [2] *and* JED W. ATKINSON [2]

[1]Instituto Patagónico de Geología y Paleontología (IPGP CCT CONICET−CENPAT), Bvd. Brown 2915, U9120CD, Puerto Madryn, Chubut, Argentina; e-mail; mferrari@cenpat-conicet.gob.ar.

[2]School of Earth and Environment, University of Leeds, Leeds, LS2 9JT, UK; e-mails: c.t.s.little@earth.leeds.ac.uk, gy12jwa@leeds.ac.uk.

Abstract. Here we describe a new late Toarcian (Lower Jurassic) marine gastropod fauna from rocks of the Cleveland Basin exposed on the North Yorkshire coast of England. The fossil assemblage comprises sixteen species, of which three are new: *Katosira*? *bicarinata* sp. nov., *Turritelloidea stepheni* sp. nov. and *Striactaenonina elegans* sp. nov. Four species are described in open nomenclature as *Tricarilda*? sp., *Jurilda* sp., *Cylindrobullina* sp. and *Cossmannina* sp. The other species have previously been described: *Coelodiscus minutus* (Schübler *in* Zieten), *Procerithium quadrilineatum* (Römer), *Pseudokatosira undulata* (Benz in von Zieten), *Palaeorissoina* aff. *acuminata* (Gründel, 1999b), *Pietteia unicarinata* (Hudleston), *Globularia* cf. *canina* (Hudleston), *Striactaenonina* cf. *richterorum* Schulbert & Nützel, *Striactaenonina* aff. *tenuistriata* (Hudleston) and *Sulcoactaeon sedgvici* (Phillips). Most of these species are the earliest records of their respective genera and show palaeobiogeographical connections with contemporary gastropod associations from other regions of Europe and South America. The taxonomic composition of the late Toarcian Cleveland Basin gastropod assemblage differs substantially from the faunas of the late Pliensbachian and early Toarcian *Tenuicostatum* Zone, showing the strong effect of the early Toarcian mass extinction event on the marine gastropod communities in the basin. Only a few gastropod species are shared between the late Toarcian faunas and the much more diverse Aalenian gastropod faunas in the Cleveland Basin, suggesting there was a facies control on gastropod occurrences at that time. This is also a potential explanation for the taxonomic differences between the late Toarcian gastropod faunas in the Cleveland Basin and those in France, and Northern and Southern Germany.

Key words: Gastropods, taxonomy, late Toarcian, Cleveland Basin, faunal recovery, evolution.

MASS extinction events have had major effects on the pattern of biotic evolution on Earth, both by reducing standing diversity and by opening ecospace for subsequent radiations of surviving organisms. While much palaeontological research effort has been expended over the past 40 years elucidating patterns of extinction and identifying cause-and-effect mechanisms for the major mass extinction events, much less is known about biotic recovery patterns, including rates and the structure of post-extinction communities. One of the mass extinction events identified in the 1980s in the Sepkoski Phanerozoic diversity curves was in the Lower Jurassic at the Pliensbachian-Toarcian stage boundary, resulting in the loss of 15-20% of marine families and genera (Sepkoski 1996). This event has been studied extensively and is now regarded to have occurred mainly in the early Toarcian, co-incident with the deposition of laminated black shale facies across the NW European area, a negative carbon isotope excursion and progressive global warming, probably due to volcanogenic CO_2 released from the Karoo-Ferrar Volcanic Province (see Thibault *et al*. 2018 and Xu *et al*. 2018 for recent reviews). Although the early Toarcian extinction event is best known from the European record, it has been also identified in Canada, Chile, Siberia and Tibet (Aberhan & Fürsich 2000; Wignall *et al*. 2006; Zakharov *et al*. 2006; Al Suwaidi *et al*. 2016, Martindale & Aberhan 2017). The early Toarcian laminated black shale facies in NW Europe (referred to often as the Toarcian Oceanic Anoxic Event) represents periods of time when oxygen levels in the sediments and probably periodically much of the contemporary water column fell to levels below which animals could not live, punctuated with short duration oxygenation events (e.g. Röhl *et al*. 2001). This facies is well represented as the 'Jet Rock' (Mulgrave Shale Member; Powell 2010) in the expanded Toarcian sections in the Cleveland Basin, cropping out in superb coastal exposures of North Yorkshire. Several very comprehensive palaeontological studies have been made of these globally important rock sections, establishing both the pattern and rates of biotic extinction during the early Toarcian event, using macrofossil range chart data (e.g. Little 1996; Harries & Little 1999; Caswell *et al*. 2009; Danise *et al*. 2013). Up until recently very little was known about the biotic recovery from the early Toarcian extinction event in the Cleveland Basin, in part because of local sedimentary gap in the middle Toarcian. Therefore, an extensive new collection of marine macrofossils was made from the Ravenscar section on the North Yorkshire coast (Figure 1), which has a complete middle to late Toarcian sequence, representing four ammonite zones and around 5.1 million years of geological time (Knox 1984; Powell 2010; Boulila *et al*. 2014). After the bivalves, gastropods form the second largest proportion of the benthic macrofossils in this collection in terms of diversity, and this paper provides a systematic description of the gastropod taxa represented. In addition, we compare the taxonomic affinities of this gastropod fauna with pre-extinction and Aalenian gastropod faunas in the Cleveland Basin, and contemporary gastropod occurences from other regions of Europe and South America, to assess post-extinction recovery and Toarcian palaeobiogeographical connections, respectively.

GEOLOGICAL SETTING

The Cleveland Basin hosts one of the most expanded Toarcian rock sections in the UK, yet across much of the basin the Lower Jurassic sequence is terminated by an erosive period during the Middle Jurassic (Powell 2010). This resulted in the Aalenian-aged Dogger Formation resting unconformably on the middle Toarcian Alum Shale Member of the Whitby Mudstone Formation (Figure 1). However, within the Peak Trough, which was actively subsiding during the Lower Jurassic, a middle to late Toarcian sequence was preserved from erosion, and is exposed in the sea cliffs and foreshore between Ravenscar and Blea Wyke, North Yorkshire (Figure 2). This sequence consists of the uppermost members of the Whitby Mudstone Formation and the Blea Wyke Sandstone Formation

(Figure 2), and represents a regressive sedimentary sequence, from mudstones to fine sandstones (Knox 1984; Powell 2010). The late Toarcian rocks are capped by the oolitic facies of the Dogger Formation, probably disconformably, as the last Toarcian sub-zone appears to be missing from the sequence here (Knox 1984). Descriptions of the Ravenscar section in the 19th and early 20th century tended to group the Blea Wyke Sandstone Formation with the Dogger Formation (discussed in detail by Dean 1954), rather than the underlying Lower Jurassic sequence. Partly for this reason, there have been relatively few non-ammonite palaeontological studies from late Toarcian Ravenscar section. In the case of the gastropods, Tate and Blake (1876) listed two species from the Peak Mudstone and Fox Cliff Siltstone Members of the Whitby Mudstone Formation (their Ammonites jurensis Zone), Hudleston (1884, 1887) described and figured two species from the Yellow Sandstone Member of the Blea Wyke Sandstone Formation (his 'Yellow Sandstones') and Dean (1954) listed a single species from the Peak Mudstone Member of the Whitby Mudstone Formation (his 'Striatulus Shales').

MATERIAL AND METHODS

In the summer of 2013 and 2017 JWA and CTSL collected 24,006 macrofossil specimens from 37 sample points covering 45 metres of the Ravenscar section from the top of the Alum Shale Member of the Whitby Mudstone Formation to the top of the Blea Wyke Sandstone Formation [Figure 2; Ferrari et al. (2020, table 1)]. Of the macrofossils 477 were gastropods. An additional three gastropod specimens collected in 2017 from loose blocks of the Grey Sandstone Member were donated by Rob Taylor. The gastropods were preserved in two modes: 1) specimens preserved with recrystallized shells, mainly in the Whitby Mudstone Formation, but also some in the Blea Wyke Sandstone Formation; 2) specimens preserved as external moulds in mineralized patches of shells in the Yellow Sandstone Member. Representative specimens from these shell patches were subsequently cast at the University of Leeds using silicone rubber. Some of the larger gastropod specimens were whitened using ammonium chloride; the smaller specimens were imaged using a scanning electronic microscopy (SEM) at ALUAR (Aluminio Argentino, Pto. Madryn, Chubut, Argentina)

The newly collected data was augmented with gastropod occurrences from the Toarcian and Aalenian rocks of the Yorkshire coast sections listed in Tate & Blake (1876), Hudleston (1887─1896) and Gründel *et al*. (2011).

Institutional abbreviations. YORYM, Yorkshire Museum, England.

SYSTEMATIC PALAEONTOLOGY

Subcclass CAENOGASTROPODA Cox, 1960

Family COELODISCIDAE Schulbert, Nützel & Gründel in Schulbert & Nützel, 2013

Genus COELODISCUS Brösamlen, 1909

Type species. *Euomphalus minutus* Schübler *in* Zieten, 1832; from the Lower Jurassic of Germany.

Remarks. The genus *Coelodiscus* is known from the Pliensbachian to the Aalenian of Europe, but is most abundant in the Toarcian Posidonienschiefer of Southern Germany (Brösamlen 1909). *Coelodiscus* is small, multi-whorled and thin-shelled. The teleoconch of the type species has fine spiral ornament (Schulbert & Nützel 2013). Jefferies & Minton (1965), Bandel & Hemleben (1987) and Schulbert & Nützel (2013) interpreted *Coelodiscus* as having had a planktonic, rather than benthic lifestyle. Recently, Teichert & Nützel (2015) recognized the type species of the genus (*C. minutus*) as being the oldest known holoplanktonic gastropod. This is the first certain occurrence of the genus in the late Toarcian of the UK.

Occurrence. Early Pliensbachian-early Aalenian; Southern Germany, Northern Switzerland, England and Argentina.

Coelodiscus minutus (Schübler *in* Zieten, 1833)

Figures 3 A─E

?2001 *Coelodiscus* sp. Gründel, p. 59, pl. 5, figs. 9─10.

2013 *Coelodiscus minutus* Schübler *in* Zieten, 1833; Schulbert & Nützel, p. 738, fig. 12A─C.

2015 *Coelodiscus minutus* Schübler *in* Zieten, 1833; Teichert & Nützel, fig. 2.

Material. YORYM: 2019.315 and YORYM: 2019.316; two specimens preserved as external moulds.

Description. Planispiral, wider than high, small- sized, very low- and slightly concave spired shell. The protoconch consists of one convex, globose whorl (Fig. 3 C). The teleoconch consists of five convex whorls; last whorl markedly more expanded than the spire. The upper portion of last whorl strongly convex, becoming straight to slightly convex to the lower portion. Suture deeply incised in a deep spiral furrow. The shell lacks spiral and collabral elements. Aperture is holostomatous and oval, forming an acute adapical channel. Basal and umbilical characters are unknown.

Dimensions (mm). YORYM: 2019.315: height, 1.83; width, 2.14. YORYM: 2019.316: height, 1.73; width, 2.18.

Remarks. Coelodiscus minutus (Schübler *in* Zieten, 1833) has been reported by Schulbert & Nützel (2013) and Teichert & Nützel (2015) from the early-late Toarcian and early Aalenian of Southern Germany. According to the description in Bandel & Hemleben (1987) and Teichert & Nützel (2015), *C. minutus* is ornamented by fine longitudinal spiral cords (striae) with 33 striae on last whorl, and smooth opisthocyrt growth lines with a concave sinus near the suture. However, in the two specimens here described the typical spiral cords are not visible.

Gründel (2001, p. 59, pl. 5, figs. 9─10) reported *Coelodiscus* sp., from the Lower Jurassic (early Pliensbachian) of Argentina, which is also very similar to *C. minutus* in size and shell morphology; here we include Gründel's species as a doubtful synonym of *C. minutus*. Another very similar species to *C. minutus* is *C. brevispira* Conti & Fischer, 1984, from the Middle Jurassic (Bajocian) of Italy. *C. brevispira*, however, lacks the spiral cords on the teleoconch whorls (Conti & Fischer 1984; p. 134, pl. 1, figs. 12a─c, 13a─b). Another species possibly comparable to *C. minutus* is *C. wrightianus* Tate in Tate & Blake, 1876, reported from the Lower Jurassic (early Pliensbachian) of England; however, the authors did not describe nor figure the species.

Occurrence. Lower Jurassic (early Pliensbachian)-Middle Jurassic (early Aalenian); Andean region of Argentina, Southern Germany, Northern Switzerland and England.

Superfamily CERITHIOIDEA Fleming, 1822

Family PROCERITHIIDAE Cossmann, 1906

Genus PROCERITHIUM Cossmann in Chartron & Cossmann, 1902

Type species. *Procerithium quinquegranosum* Cossmann, 1902; from the Lower Jurassic (Hettangian) of France.

Remarks. Here we follow the diagnosis of Gründel (1999a, p. 3) for the genus.

Occurrence. Lower Jurassic (Hettangian)–Lower Cretaceous (Barremian); Europe, Africa, New Zealand, Asia, Antarctica (?), and South America.

Procerithium quadrilineatum (Römer, 1836)

Figures 3 F—L

1876 *Cerithium quadrilineatum* Römer, 1836; Tate & Blake, p. 351.

1889 *Cerithium quadrilineatum* Römer, 1836; Hudleston, p. 145, pl. 8, fig. 1

Material. YORYM: 2019.317, YORYM: 2019.318, YORYM: 2019.319 (Fig. 3I-L), YORYM: 2019.320 (Fig. 3F-G), YORYM: 2019.321, YORYM: 2019.322, YORYM: 2019.323, YORYM: 2019.324, YORYM: 2019.325, YORYM: 2019.326, YORYM: 2019.327, YORYM: 2019.328, YORYM: 2019.329, YORYM,: 2019.330, YORYM: 2019.331, YORYM: 2019.332, YORYM: 2019.333, YORYM: 2019.334, YORYM: 2019.335, YORYM: 2019.336, YORYM: 2019.337, YORYM: 2019.338, YORYM: 2019.339, YORYM: 2019.341, YORYM: 2019.342, YORYM: 2019.343; twenty six specimens preserved as external moulds. YORYM: 2019.340; one specimen preserved as a recrystallized shell.

Description. Turriculate, slender, small-sized and high-spired shell. Protoconch consists of 2-4 conical and convex whorls with a width of 0.36 mm and height of 0.41 mm. First two protoconch whorls smooth; fourth whorl bears a very weak abapical spiral cord near suture (Fig. 3 L). Clear demarcation between protoconch and teleoconch. Teleoconch consists of 7-10 whorls. Sutural ramp narrowly horizontal on earliest whorls, becoming sloped and inclined 45º from suture toward mature growth stages. Suture deeply incised in a spiral furrow; a very thin, almost smooth and adapical spiral cord borders suture on mature whorls. Four earliest teleoconch whorls are flattened; at mature growth stages the whorls become slightly convex. Earliest 2-3 teleoconch whorls ornamented by straight to slightly opisthocline axial ribs; on mature whorls axial ribs become strongly opisthocline to opisthocyrt, and number 14/16 per whorl. From third teleoconch whorl to mature growth stages axial ribs intercepted by 5-6 regularly spaced spiral cords forming small and rounded nodes at crossing points. Shell base slightly convex and ornamented by several (4-7) smooth and acute spiral cords. Fine and weak collabral lines visible on shell surface. Aperture is holostomatous and oval.

Dimensions (mm). Table 1.

Remarks. Our specimens seem to be conspecific with *Cerithium quadrilineatum*, Römer, 1836 described from the 'Yellow Sandstones' at Ravenscar by Hudleston (1889), although it is worth noting that the specimen illustrated by Hudleston (1889, pl. 8, fig. 1) is a fragmentary teleoconch without juvenile whorls. Tate & Blake (1876) also recorded this species from the highest beds of the Alum Shale in the Lofthouse Alum Works and in the Blea Wyke Beds. Based on the diagnosis of Gründel (1999a) for *Procerithium*, our specimens definitely belong to this genus, because they also have 'protoconch conical with several whorls, at first smooth, later with one spiral near to the abapical suture…First teleoconch whorl only with distinct axial ribs. Spirals become visible on the second teleoconch whorl or later'. Our specimens also show some diagnostic features of the genus *Rhabdocolpus* (see diagnosis in Gründel 1999), including 'a sutural ramp nearly horizontal or sloping. The outline of the teleoconch whorls is straight to convex…axial ribs at first straight, later opisthocyrt…their crossing point with the spirals are nodose…base convex with 5-7 spirals…aperture oval'. However, representatives of *Rhabdocolpus* have a conical protoconch with two spirals on later whorls, a character that is absent in our specimens, which instead have the protoconch typical of *Procerithium*.

P. quadrilineatum is very similar to *P. muricatum* (Sowerby, 1825) (Hudleston, 1887, p. 146, pl. 8, figs. 2 a, b), from the Dogger Formation (early Aalenian) of England. However, *P. quadrilineatum* is larger, has fewer spiral cords (about 4 or 5 per whorl) and has adapical spiral cords that are slightly stronger than the others. *P. compactum* Gründel, 1999a (p. 4, pl. 1, figs. 7─9; Schulbert & Nützel 2013, p. 742, fig. 14H─J), from the late Toarcian and early Aalenian of Germany also resembles *P. quadrilineatum*. However, *P. compactum* has a protoconch with slightly more convex whorls, a more step-like or gradate shell outline with broader sutural ramp on juvenile whorls, weaker and less rounded nodes at the crossing points of the axial and spiral elements, and a pronounced and strongly nodular adapical spiral cord on the upper portion of the whorl, bordering the narrow ramp. *P. oderinensis* Gründel, 1999a (p. 5, pl. 1, figs. 10─14; Gründel 2007, p. 239, pl. 4, fig. J─K), from the late Toarcian and early Aalenian of northern Germany differs from *P. quadrilineatum* in having two strong spiral cords on earliest teleoconch whorls at the adapical and abapical position, and more acute nodes at the crossing points with the axial ribs. *P. pseudocostellatum* (d'Orbigny, 1850) (Gatto *et al*. 2015, p. 891, fig. 9c─s), from the Toarcian-Aalenian of Southern France, differs from *P. quadrilineatum* in having a more gradate shell, stronger axial ribs, and more conspicuous nodes at the crossing point of the axial and spiral elements. *P. nulloi* (Ferrari, 2009) (p. 457; 2012, p. 328), from the Pliensbachian-Toarcian of Argentina differs from *P. quadrilineatum* in being larger, and having spiral ornament predominant on adult whorls, where the axial ribs become weaker *P. quadrilineatum* bear some resemblance to those of *Rhabdocolpus (Rhabdocolpus) multinodosum* Gründel, 1999a (p. 7, pl. 1, figs. 15─20), from the Middle Jurassic (late Bathonian) of Poland, but the latter species has a slightly weaker and narrower sutural ramp, and the crossing points of the axial and spiral elements are only weakly nodose. *R. patagoniensis* (Ferrari, 2012) (p. 329, figs. 4G-P, 5A─K, as *Procerithium (Rhabdocolpus) patagoniensis* Ferrari, 2017, p. 6, fig. 2.14─2.17), from the Sinemurian-Toarcian of Argentina, differs from *P. quadrilineatum* in having a step-like outline shell with a broader and horizontal sutural ramp, and weaker and less rounded nodes at the crossing points of the axial and spiral elements. Finally, *P. quadrilineatum* is similar to *R. (Infacerithium) excavatus* Ferrari & Damborenea, 2015 (p. 635, fig. 2. 20─22), from the Middle Jurassic (early Bajocian) of Argentina. Both species share similar outline shell, with a narrow and sloped sutural ramp, and opisthocyrt axial ribs on mature whorls. However, the Argentinian species has slightly stronger nodes on the adapical spiral of mature whorls.

Occurrence. Lower Jurassic (late Toarcian); Northern England, Germany and France.

Suborder PTENOGLOSSA Gray, 1853

Superfamily ZYGOPLEUROIDEA Wenz, 1940

Family ZYGOPLEURIDAE Wenz, 1940

Subfamily AMPEZZOPLEURINAE Nützel, 1998

Genus KATOSIRA Koken, 1892

Type species. *Chemnitzia periniana* d'Orbigny, 1853; from the Lower Jurassic (Pliensbachian) of France.

Remarks. The type species designation for the genus *Katosira* was discussed by Nützel & Gründel (2015) and they argued that two species have been considered in the literature as the types of *Katosira*: *K. periniana* (d'Orbigny, 1853) from the Lower Jurassic (Pliensbachian) of France, and *K. fragilis* Koken, 1892, from the Upper Triassic (Carnian) of the Southern Alps. Nützel & Gründel (2015) examined the holotypes of both species and observed that the axial ribs are continuous from suture to suture in all teleoconch whorls, and that there is no reduction of the axial ribs during ontogeny. However, they suggest that the morphology of *K. fragilis* is still not known completely and that the subsequent designation of *Chemnitzia periniana* as type species of *Katosira* by Cossmann (1909) is valid.

Occurrence. Upper Triassic (Carnian)-Upper Jurassic (Oxfordian); cosmopolitan.

Katosira? *bicarinata* sp. nov.

(Fig. 3 M─R)

2007a *Katosira* sp. Gründel, p. 83, pl. 4, fig. 15─17.

Derivation of name. Referring to the two strong and nodular spiral cords bordering the sutures on mature whorls.

Type material. Holotype, YORYM: 2019.344 (Fig. 3M-N); paratype, YORYM: 2019.345 (Fig. 3Q-R); complete teleoconch and juvenile specimen preserved as external moulds.

Additional material. YORYM: 2019.346 (Fig. 3O), YORYM: 2019.347 (Fig. 3P), YORYM: 2019.348, YORYM: 2019.349, YORYM: 2019.350, YORYM: 2019.351, YORYM: 2019.352; seven fragmentary specimens preserved as external moulds.

Type locality. Ravenscar, North Yorkshire, England.

Type level. Late Toarcian (Blea Wyke Sandstone Formation, Yellow Sandstone Member), Cleveland Basin.

Diagnosis. Turriculate, slender shell; teleoconch whorls with opisthocline to opisthocyrt axial ribs; spiral elements missing on earliest whorls appearing weakly on third or fourth whorl; small and rounded nodes at crossing points of axial and spiral elements; adapical and abapical cords nodular and stronger than others; base ornamented by spiral cords; aperture holostomatous and oval.

Description. Turriculate, slender, small-sized and high-spired shell. Protoconch fragmentary, consisting of two (probably three originally) convex and smooth whorls (Fig. 3 Q─R); height 0.47 mm, width 0.38 mm. Clear demarcation between protoconch and teleoconch. Teleoconch consists of eight whorls; outline of earliest whorls flattened and becomes slightly convex abapically toward mature whorls. Suture incised. First teleoconch whorl begins with opisthocline to opisthocyrt axial ribs which run from suture to suture; pattern conservative throughout ontogeny. Juvenile whorls have 16-17 axial ribs per whorl; mature whorls have 19-20 axial ribs per whorl. Spiral cords missing on earliest whorls and appear weakly at the third or fourth whorl. Spiral ornament of 7-8 regularly spaced cords that intercept axial ribs on mature whorls to form small and rounded nodes at crossing points. Adapical and abapical spiral cords border suture of each whorl and are stronger than other spiral cords. Nodes clearly more conspicuous and rounded on the two stronger spiral cords (Fig. 3 Q─R). Shell base conoidal with moderately convex surface and ornamented by seven regularly spaced spiral cords. Aperture holostomatous and oval.

Dimensions (mm). Table 2.

Remarks. The type species *Katosira periniana* (d'Orbigny, 1853) (p. 36, pl. 243, figs. 1─2; Fischer & Weber 1997, p. 14, pl. 1, fig. 5; Szabó 2009, p. 93, fig. 84 E─I; Nützel & Gründel 2015, p. 16, pl. 8 F─I) differs from *Katosira*? *bicarinata* sp. nov. in being larger, having a large number of spiral cords on all teleoconch whorls, and with axial ribs that are slightly less opisthocryt on juvenile whorls and becoming obsolete toward mature growth stages. *K. fragilis* Koken, 1892 (in Nützel & Gründel 2015, p. 16 pl. 8 F─I) is also higher-spired than *K.*? *bicarinata* sp. nov., has indistinct spiral cords, and strong and slightly orthocline axial ribs. *K. suessii* (Stoliczka, 1861) (p. 163, pl. 1, fig. 2; Szabó 2009, p. 93, fig. 85), from the Lower Jurassic (late Sinemurian) of Hungary, differs from *K.*? *bicarinata* sp. nov. in having a more convex periphery below the mid-whorl, more dense and feebly parasigmoidal axial ribs, and two abapical spiral threads with tubercles. *K. hierlatzensis* (Stoliczka, 1861) (p. 164, pl. 1, figs. 3 a─b; Szabó 2009, p. 94, fig. 86), from the Lower Jurassic (Sinemurian-Pliensbachian) of Austria, has more developed tubercles at the crossing points of the axial ribs, and a sub-sutural spiral swelling; it also has more dense collabral growth lines. Another comparable species to *K.*? *bicarinata* sp. nov. is *K. anaroides* (Schmidt, 1905) (p. 188, pl. 9, figs. 28─29; Kaim & Gründel, 2006, p. 143, text-fig. 19A─C), from the Upper Jurassic (Oxfordian) of Poland. The latter species, however, has a less slender shell with more convex whorls, and a strong axial ornament consisting of 6-8 orthocline to opisthocline ribs, which occur throughout ontogeny. *K. basistriata* Gründel, 2007b (p. 13, pl. 4, fig. 7), from the Lower Jurassic (Sinemurian) of Germany, is very similar to *K.*? *bicarinata* sp. nov., but differs in having parasigmoidal axial ribs on last whorl. *K. contii* Fischer *et al*., 2002 (p. 450, fig. 4.10─11), from the Lower Jurassic (Sinemurian) of Italy differs greatly from *K.*? *bicarinata* sp. nov. in being much larger, having stronger spiral and nodular elements, and less developed opisthocyrt axial ribs. Finally, *K.*? *bicarinata* sp. nov. is also very similar to *Camponaxis jurassica* Nützel & Gründel (2015), from the Lower Jurassic (late Pliensbachian) of southern Germany. However, *Camponaxis jurassica* has a clearly developed heterostrophic larval shell. This character is not clearly visible in our specimens and, thus, *bicarinata* is retained doubtfully within *Katosira*.

Occurrence. Lower Jurassic (late Pliensbachian-late Toarcian); Northeastern Germany and England.

Genus PSEUDOKATOSIRA Nützel & Gründel, 2007

Type species. *Turritella undulata* Benz in von Zieten, 1832, Pliensbachian, Southern Germany.

Remarks. According to Nützel & Gründel (2007) the genus *Pseudokatosira* is monotypic. There are many Mesozoic species that could belong to *Pseudokatosira*, but the diagnostic generic characters are unknown for most of these. *Pseudokatosira* resembles the genus *Katosira* but differs from it in several respects, e.g. *Pseudokatosira* has a marked change in teleoconch ontogeny with a reduction of the axial ribs toward mature growth stages, which also become round and nodular after several whorls.

Occurrence. Lower Jurassic (Pliensbachian-late Toarcian); Southern Germany, Hungary, Austria and England.

Pseudokatosira undulata (Benzin von Zieten, 1832)

(Fig. 3 S─U)

1832 *Turritella undulata* Benz in Von Zieten, p. 43, pl. 32, fig. 2.

2002 *Katosira undulata* (Benz, 1832); Nützel & Hornung, p. 58, pl. 1,
figs 4–5.

2007 *Pseudokatosira undulata* (Benz, 1832); Nützel & Gründel, p. 62, pl. 1, figs. 1─6.

2008 *Pseudokatosira undulata* Nützel, p. 46, pl. 2, fig. 1.

2009 *Pseudokatosira undulata* (Benz, 1832); Szabó, p. 91, pl. 84, figs. C─D,

2015 *Pseudokatosira undulata* (Benz, 1832); Nützel & Gündel, p. 16, pl. 8, fig. A─E.

Material. YORYM: 2019.353 (Fig. 3T-U), YORYM: 2019.354 (Fig. 3S), YORYM: 2019.355, YORYM: 2019.356, YORYM: 2019.357; five fragmentary specimens preserved as external moulds.

Description. Turriculate, slender, high-spired and medium-sized shell. Protoconch not preserved. Teleoconch partial, consisting of six convex whorls in most complete specimens. Suture incised. Juvenile whorls smooth and less convex than mature whorls. Mature whorls ornamented by strong and opisthocyrt axial ribs. Axial ribs strongest and almost node-like below mid-whorl. Mature whorls covered with numerous irregularly spaced spiral cords, numbering 13-18 per whorl and intercalated by spiral furrows. Weak opisthocyrt collabral growth linesvisible on last whorl. Shell base strongly convex and ornamented by 13-14 regularly spaced spiral cords. Aperture strongly oval, higher than wide, elongated with acute anterior siphonal canal.

Dimensions (mm). YORYM: 2019.354: height, 10.54*; width, 5.38. YORYM: 2019.355: height, 8.77*; width, 2.74*. YORYM: 2019.353: height, 8.33*; width, 4.11. YORYM: 2019.357: height, 5.03*; width, 2.79*. YORYM: 2019.356: height, 11.97; width, 4.46. * = partial specimens.

Remarks. Based on the updated description of *Pseudokatosira undulata* in Nützel & Gründel (2015) our specimens belong to this species, because they are large and high-spired with broad, round axial ribs, which become increasingly nodular and do not extend to adapical suture on the mature teleoconch. *P. undulata* has been reported from Southern Germany (e.g., Quenstedt 1884, Brösamlen 1909, Nützel & Hornung 2002, Nützel & Gründel 2007), Hungary (Szabó 1983), Austria (Szabó 2009) and England (Todd & Munt 2010). The specimens described by Szabó (2009) as *Pseudokatosira*? aff. *undulata* from the Hierlatz Limestone (Late Sinemurian, Austrian Alps) resemble *P. undulata*, but lack node-like ribs on mature teleoconch whorls, so their specific identity remains unclear.

Occurrence. Lower Jurassic (Pliensbachian-Toarcian); Southern Germany, Hungary, Austria and England.

Superfamily RISSOIDEA Gray, 1847

Family PALAEORISSOINIDAE Gray, 1847

Genus PALAEORISSOINA Gründel, 1999b

Type species. *Palaeorissoina compacta* Gründel, 1999b; from the late Bajocian and Callovian of Northeast Germany and Poland.

Occurrence. Lower Jurassic (Toarcian)-Lower Cretaceous (Valanginian).

Palaeorissoina aff. *acuminata* (Gründel, 1999b)

(Fig. 3 V─X)

1990. *Rissoina acuta* (Sowerby, 1818); Gründel 1990, p. 1145, pl. 2: 8 [non Sowerby 1818: 230, pl. 609: 2 - *Bralitzia acuta* (Sowerby, 1818)].

1999b. *Palaeorissoina acuminata* Gründel; p. 97, pl. 4: 12–16.

2004 *Bralitzia acuminata* (Gründel, 1999b); Kaim, p. 80, fig. 61.

Material. YORYM: 2019.358 and YORYM: 2019.359; two specimens preserved as external moulds.

Description. Turriculate, slender, small-sized and high-spired shell. Protoconch trochospiral, formed of three smooth and strongly convex whorls; height 0.35 mm, width 0.36 mm. Clear demarcation between protoconch and teleoconch. Teleoconch formed of 5-6 flattened to slightly convex whorls. Suture incised. Ornament predominantly strongly opisthocline to opisthocyrt acute axial ribs, running from suture to suture. Shell base slightly convex to flattened; aperture strongly oval.

Dimensions (mm). YORYM: 2019.358: height, 3.77*; width, 1.42. YORYM: 2019.359: height, 4.08; width, 1.44. * = partial specimens.

Remarks. Our specimens are very similar in shell shape and ornamentation to *Palaeorissoina acuminata* Gründel, 1999b (p. 97, pl. 4, fig. 12-16; Kaim, 2004, as *Bralitzia acuminata*, p. 80, fig. 61), from the Middle Jurassic (Callovian) of Germany. Accordig to the diagnosis of Gründel (1999b), this species has a highly conical protoconch without sculpture. The shell is slender with many whorls with the apical part sharpened. Teleoconch whorls with strong and symmetrical axial ribs, and the spiral cords are mostly densely packed. In our material, the spiral cords are not visible (most probably due bad preservation); thus, it is left in open nomenclature. *Palaeorissoina tenuistriata* Gründel (1999b) (p. 99, pl. 2 fig. 4.11), differs from *P*. aff. *acuminata* in having more developed and visible spiral striae in all teleoconch whorls, and weak nodes in the middle of axial ribs on mature whorls.

Occurrence. Early Lower Jurassic (Late late Toarcian)–Middle Jurassic (Callovian); Germany, Poland and England.

Superfamily STROMBOIDEA Rafinesque, 1915

Family APORRHAIDAE Gray, 1850

Genus PIETTEIA Cossmann, 1904

Type species. *Rostellaria hamus* Eudes−Deslongchamps, 1842: 173; original designation. Bajocian (Middle Jurassic), Bayeux, France.

Remarks. Kaim (2004, p. 74) characterized representatives of the genus *Pietteia* Cossmann, 1904. This genus is mostly known from the Middle and Upper Jurassic of Europe and Africa (Cox 1965; Szabó 1983; Conti & Fischer 1984; Conti & Monari 1986; Kaim 2004; Gründel 2003; Gründel *et al*. 2012), but few reports have given accurate stratigraphical data about its occurrence in the Lower Jurassic. One exception is *Pietteia* (*Trietteia*?) *mipa* (De Gregorio, 1886) which Conti & Szabó (1989) described from different stratigraphical levels in the latest Toarcian (Aalensis Zone) to the earliest Bajocian (Discites Subzone) of Italy.

Occurrence. Lower Jurassic-Upper Jurassic; Europe.

Pietteia unicarinata (Hudleston, 1884)

(Fig. 4 A─L)

1884 *Alaria unicarinata* Hudleston, p. 149, pl. 6, fig.s 1, 2, 2a.

1887 *Alaria unicarinata* Hudleston, p. 118, pl. 4, fig. 13a, b, c.

Material. YORYM: 2019.360 (Fig. 4A-C), YORYM: 2019.361 (Fig. 4E), YORYM: 2019.362 (Fig. 4D), YORYM: 2019.363, YORYM: 2019.364 (Fig. 4K-L), YORYM: 2019.365, YORYM: 2019.366, YORYM: 2019.367, YORYM: 2019.368, YORYM: 2019.369 (Fig. 4F), YORYM: 2019.370, YORYM: 2019.371, YORYM: 2019.372, YORYM: 2019.373, YORYM: 2019.374, YORYM: 2019.375, YORYM: 2019.376 (Fig. 4G-H); seventeen specimens preserved as external moulds. YORYM: 2019.377 (Fig. 4I-J); one teleoconch preserved as a recrystallized shell.

Emended diagnosis. Step-like or gradate and small-sized shell; protoconch 1 of one smooth and convex whorl; protoconch 2 of two smooth and convex whorls; first teleoconch whorl with opistocline axial ribs and without spiral elements; from second teleoconch whorl to mature growth stages spiral cords and axial ribs are predominant, with pointed nodes at periphery; axial ribs missing on last whorls; base angular, ornamented by six spiral cords; aperture oval with strongly developed and expanded abapically siphonal channel; outer lip with long spine-like extension ornamented by four regularly spaced spiral cords.

Description. Gradate, angular in shape, small-sized and moderately high-spired shell. Protoconch 1 partial, formed of one smooth and convex whorl. Protoconch 2 formed of two smooth and strongly convex whorls; height 1.01 mm, width 0.83 mm. Clear demarcation between protoconch 2 and first teleoconch whorl (Fig. 4 D, F). Teleoconch formed of up to seven whorls; first teleoconch whorl convex; toward mature growth stages whorls become strongly angular in outline. Suture incised. Ornament pattern changes during ontogeny. First teleoconch whorl ornamented by 16 slightly opisthocline axial ribs without spiral elements; toward second teleoconch whorls axial ribs intercepted by two very weak spiral cords forming small nodes at crossing points. From third to mature whorls ornament comprises opisthocline axial ribs, more prominent over the outer face of whorls. Mature whorls strongly angular; axial ribs reduced to opisthocline pointed nodes visible on whorl peripheries. On mature whorls ramp flattened, inclined 45º and ornamented by up to six regularly spaced spiral cords, intercalated by spiral furrows. Outer face of mature whorls inclined abaxially and ornamented by four spiral cords. Nodes at periphery of penultimate whorl strongly pointed and acute, 16 in number. Last teleoconch whorl strongly angular with periphery delimited by smooth and acute spiral keel without peripheral nodes. Shell base flattened and angular, delimited on the outer face by strong and acute spiral cord; ornamented by six spiral cords with spiral furrows between. Aperture oval with strongly developed siphonal channel, expanded abapically. Outer lip bears long spine-like extension ornamented by four regularly spaced spiral cords (Fig. 4 G─H).

Dimensions (mm). Table 3.

Remarks. This species was originally assigned by Hudleston (1884) to the genus *Alaria*. We transfer it here to *Pietteia* Cossmann, 1904 following Kaim (2004) (see above). *Alaria arenosa* Hudleston, 1884 (p. 198, pl. 7, fig 7; Hudleston 1887, p. 110, pl. 4, fig. 1), also from Blea Wyke Sandstone Formation at Ravenscar, differs from *Pietteia unicarinata* in having a larger, more slender and turriculate shell, two spiral keels per whorl with the adapical keel stronger and with more developed tubercles than the abapical keel, and having a strongly expanded siphonal canal. Moore (1866) described three aporrhaid species from Toarcian sections in the Ilminster area of Somerset in Southern England that should be compared to *P. unicarinata*. *Alaria angulata* Moore, 1866 (p. 197, pl. 4, fig. 4) differs from *P. unicarinata* in lacking pointed nodes at the peripheral cords on mature whorls, and in lacking opisthocline axial ribs on juvenile whorls, being ornamented by spiral elements only. *Alaria coronata* Moore, 1866 (p. 198, pl 4, fig. 3) differs from the *P. unicarinata* in having small and regular granulation in the periphery of each whorls. *Alaria unispinosa* Moore, 1866 (p. 197, pl. 4, figs. 1, 2), like *P. unicarinata*, has an expanded siphonal channel and a spine-like projection extended from the adapical margin of the outher lip. However, in Moore's species the lateral projection is smooth without spiral cords, and is finer. It curves upwards and extends more than the diameter of the shell beyond the margin. *A. unispinosa* also lacks nodular and axial elements on the shell surface, being ornamented only by spiral cords. *P. unicarinata* can be easily distinguished from *P. (Trietteia?) mipa* (De Grogorio, 1886) (in Conti & Szabó 1989; p. 37, pl. 2, figs. 12─14) (see above) because the Italian species has a higher-spired shell, more convex whorls, and a strongly reticulate ornament pattern consisting of spiral cords intercepted by collabral opisthocyrt growth lines and small spiny nodes at the whorl angulations; these characters are all missing in *P. unicarinata*. *P. unicarinata* also has a resemblance to *P. hamus* (Eudes-Deslongchamps, 1843) (in Gründel 2003; p. 83, pl. 11, fig. 6─8, 12─15), from the Middle Jurassic (Bathonian) of Southern Germany and France, but *P. hamus* is much larger, has better developed axial ribs and more pointed nodes at the periphery of mature whorls, and the peripheral spiral keel on the final whorls is stronger. *P. trispinigera* Szabó, 1983 (p. 40, pl. 3, figs. 12─13; Conti & Fischer, 1984; p. 156, pl. 5, fig. 23 as *P. apenninica* Conti & Fischer, 1984), from the Middle Jurassic (Bajocian) of Hungary and Italy, differs from *P. unicarinata* in being larger, with a higher spire, a reticulate ornament pattern formed by opisthocyrt growth lines and axial ribs restricted only to the juvenile shell, parabolic nodes at the angulation up to the penultimate whorl, and embryonic whorls bearing two suprasutural (abapical) spiral cords. *P. subbicarinata* (Münster, 1844) and *P. pellati* (Piette,

1867) (in Kaim, 2004; ps. 75─76, figs. 56─57), both from the Middle Jurassic (Callovian) of Poland, are larger than *P. unicarinata*, have axial ribs and tubercles on only the earliest two teleoconch whorls. They have later teleoconch whorls ornamented only by regularly spaced spiral cords, and a stronger peripheral spiral keel on last whorl. *Pietteia* sp. (in Gründel *et al*. 2012; p. 34, pl. 8, fig. 9), from the Middle Jurassic (Bajocian) of Southern Germany, differs from *P. unicarinata* in being larger, having more convex teleoconch whorls and in being completely smooth. *P. callamus* Gründel, 2001 (p. 72, pl. 8, fig. 12─15) from the Middle Jurassic (Callovian) of Northern Germany, differs from *P. unicarinata* in having more variable axial ribs in shape and number, which run from suture to suture, giving the whorl periphery a more convex appearance, and in having a stronger peripheral keel on the last teleoconch whorl.

Occurrence. Lower Jurassic (late Toarcian)-Middle Jurassic (early Aalenian); Northern England.

Superfamily CAMPANILOIDEA Douvillé, 1904

Family AMPULLINIDAE Cossmann in Cossmann & Peyrot, 1919

Genus GLOBULARIA Swainson, 1840

Type species. *Ampullaria sigaretina* Lamarck, 1804, Eocene, France; original designation.

Remarks. Ferrari (2013) stated that specimens belonging to the genus *Globularia*, including some from the Jurassic, have been commonly referred to *Natica*, and gave reasons to keep both genera separate. Here we follow the criteria of Ferrari (2013) in recognizing *Globularia*.

Occurrence. Triassic?, Jurassic–Holocene; Cosmopolitan.

Globularia cf. *canina* (Hudleston, 1882)
(Fig. 4 M─N)

1850 *Natica lorieri* d'Orbigny: p. 190, pl. 289, fig. 6─7.

?1882 *Natica lorieri* var. *canina* Hudleston: p. 260, pl. 20, fig. 9a─b.

Material. YORYM: 2019.378; one complete teleoconch preserved as a recrystallized shell.

Description. Globose, step-like, gradate, low-spired and medium- to large-size shell. The teleoconch consist of 5 whorls. Sutural ramp narrowly horizontal and canaliculated. Earliest whorls flattened to slightly convex. Last whorl strongly convex and markedly more expanded than spire. Upper portion of last whorl slightly concave and delimited by weak angulation with the flank; outer face of last whorl strongly convex. Fine collabral lines visible on outer face of last whorl. Base strongly convex. Aperture obliquely oval with weakly developed adapical canal and slightly expanded abapical lip. Outer lip very fine and convex; columellar lip thickened. Umbilicus visible with narrow opening.

Remarks. *Globularia canina* was originally described under the genus *Natica* by d'Orbigny (1850), from the Middle Jurassic (Bajocian) of France, and it was later reported by Hudleston 1884, from the Dogger Formation (early Aalenian) (Hudleston 1884, p. 260, pl. 20, fig 9a, b). Hudleston (1884) proposed a new name for d'Orbigny species, *Natica canina*, characterized by the absence of an umbilicus, a very large aperture and sometimes having fine spiral lines on the shell surface.

The species here described as *Globularia* cf. *canina* is very similar in shell shape and ornamentation to *Natica adducta* Phillips, 1829 (in Hudleston, 1884, p. 257, pl. 20, fig. 3) from the Dogger Formation (early Aalenian). However, *N. adducta* has more gradate spire whorls, and a more developed and horizontal sutural ramp. *Natica adducta* var. *globata* Phillips (in Hudleston 1884, p. 259, pl. 20, fig. 5─6), from the Aalenian Concavus-bed, Bradford Abbas, England, has a more globose and convex last teleoconch whorl and a more thickened columellar lip that covers the umbilical area. *Natica proxima* (Hudleston, 1882) (p. 260, pl. 20, fig. 7), from the Dogger Formation (early Aalenian), differs from *Globularia* cf. *canina* in having a more step- like spire, a thick callus on the inner lip, and more developed collabral growth lines on last teleoconch whorl. Finally, *Natica punctura* (Bean) (in Hudleston 1892, p. 264, pl. 20, fig. 14), from the Dogger Formation (early Aalenian), differs from *Globularia* cf. *canina* in having a more pointed apex with less gradate and more convex spire whorls, a reticulate ornament pattern with spiral and collabral ribs, and a less expanded last whorl.

Occurrence. Lower Jurassic (late Toarcian)-Middle Jurassic (Bajocian); Northern England and France.

Subclass HETEROBRANCHIA Burmeister, 1837

Superfamily MATHILDOIDEA Dall, 1889

Family MATHILDIDAE Dall, 1889

Genus TRICARILDA Gründel, 1973

Type species. *Mathilda* (*Tricarilda*) *plana* Gründel, 1973, original designation; Callovian; Northwestern Poland.

Remarks. Representatives of the genus *Tricarilda* Gründel, 1973 are very similar to *Jurilda* but differ in that 'the first teleoconch whorl immediately with three primary spiral ribs; middle one is strongest, and can be keel-like; additional secondary spiral ribs may lack or are abundant; microornament of spiral striae either absent or weak' (Gründel & Nützel, 2013). Kaim (2004) considered *Tricarilda* as a junior synonym of *Mathilda* Semper, 1865, based on the similar pattern of ornamentation of 'three-to-four spiral ribs on the early teleoconch'. However, here we follow Gründel & Nützel (2013) who place shells with three primary spiral ribs in *Tricarilda*.

Occurrence. Lower Jurassic (Sinemurian)–Lower Cretaceous (Valanginian); Germany, England, France, Italy, Poland, Russia, Ukraine, New Zealand.

Tricarilda? sp.

(Fig. 4 O─P)

Material. YORYM: 2019.379; one specimen preserved as an external mould.

Description. Anomphalous, turriculate, slender, small-sized. Protoconch not preserved. Teleoconch formed of six angular whorls. Suture distinct and impressed. Whorl face angulated near mid-whorl. Spiral ornament consists of three spiral cords and a fourth emerges at abapical suture. A weak spiral cord (S1), and two other spiral cords, (S2) and (S3) are much stronger than S1; S2 is located at mid-whorl. The basal spiral (BS) emerges at the suture. Spiral cords intercepted by strongly opisthocline axial ribs producing reticulate pattern. Small and rounded nodes at the crossing points of spiral and axial elements. Shell base convex with one spiral cord. Apertural characters not preserved.

Dimensions (mm). YORYM: 2019.379: height, 3.80*; width, 1.13.

Remarks. The single specimen here described could be considered to belong to the genus *Tricarilda*, but for the fact that *Tricarilda* species have three spiral cords with the centre one being keel-like and stronger than those on either side. In our specimen the two strongest spiral cords are at mid whorl (S2), and abapically (S3), so we only tentatively assign it to this genus, until more and better preserved material is discovered. The Yorkshire Toarcian *Tricarilda*? sp. is very similar in shell shape and ornamentation to *Tricarilda* sp. in Schulbert & Nützel (2013, p. 752, fig. 22E─H; Gründel, 2014, p. 80, pl. 2, figs. 10), from the Lower and Middle Jurassic (late Toarcian-early Aalenian) of Southern Germany; but that *Tricarilda* sp. has a clearly visible and strong spiral cord at mid whorl and a more angulated shell outline. *Tricarilda* sp. 1 in Gründel *et al*. (2011; p. 498, text-figure 11A─B) from the Lower Jurassic (Hettangian-Sinemurian) of the Cleveland Basin, England, differs from the Yorkshire *Tricarilda*? sp. in having two abapical and stonger spiral cords which angulated the whorls separated to each other by a a concave area. *Tricarilda toddi* Gründel *et al*., 2011 (p. 498, text-figure 12A─I), from the Lower Jurassic (late Pliensbachian) of Dorset, Southern England, differs from *Tricarilda*? sp. in being slightly larger, having more convex whorls and secondary spiral threads that are intercalated between the primary spiral threads. The axial ribs are stronger on the early teleoconch whorls, becoming weaker as growth lines toward mature whorls, and the intersections of axial and spiral elements are nodular.

Genus JURILDA Gründel, 1973

Type species. *Mathilda* (*Jurilda*) *crasova* Gründel, 1973, (=subjective junior synonym of *Promathilda* (*Teretrina*) *concava* Walther, 1951); Bajocian to Bathonian; Poland.

Occurrence. Upper Triassic?/Lower Jurassic (Hettangian) ─Lower Cretaceous; Germany, England, Italy, Poland, Ukraine.

Jurilda sp.

(Fig. 4 Q)

Material. YORYM: 2019.380; one specimen preserved as an external mould.

Description. Turriculate, small-sized. Protoconch not preserved. The fragmentary teleoconch is formed of three angular whorls. Suture distinct and impressed. Whorl face angulated near mid-whorl. Spiral ornament consists of three spiral cords. One spiral cord (S1) weak and distant from the upper suture; (S2) and (S3) on the abapical portion of the whorls and with the same strenght than (S1). Spiral cords intercepted by strongly opisthocline axial ribs producing reticulate pattern; opisthocline axial ribs become slightly orthocline between median strongest spiral cord and abapical cord. Small and rounded nodes at crossing points of spiral and axial elements. Basal and apertural characters not preserved.

Dimensions (mm). YORYM: 2019.380: height, 2.24*; width, 1.01. * = partial specimen.

Remarks. *Jurilda* sp. is very similar in shell shape and ornamentation to *Jurilda zapfi* Schulbert & Nützel (2013, p. 754, fug. 23 A-G), from the late Toarcian-early Aalenian of Germany. However, *Jurilda zapfi* has more angular whorls and more straight flanks than *Jurilda* sp. *Jurilda concava* (Walther, 1951) (in Gründel 1997 as *Promathildia concava*, p. 134, pl. 1, figs. 1-4) from the Middle Jurassic (Bathonian) of Poland, has a stronger and more acute peripheral spiral cord than *Jurilda* sp. and a more step-like teleoconch. *Jurilda* sp. (in Nützel & Gründel, 2015, p. 28, pl. 14J), from the Lower Jurassic (Pliensbachian) of Germany, has a more distinct carination low on the whorls than *Jurilda* sp. *Tricarilda* sp. 1 in Gründel *et al*., 2011 (p. 498, text-fig. 11 A-B), from the Lower Jurassic (Hettangian-Sinemurian) of England is very similar to *Jurilda* sp., but *Tricarilda* sp. 1 has two stronger and more acute spiral ribs which angulated the whorls. *Turritella (Mathilda) quadrivittata*, Phillips, 1829 (in Hudleston 1887, p. 233, pl. 17, fig. 6), from the Dogger Formation, differs from *Jurilda* sp. in having sub-globose whorls and four granular spirals on each whorl. Finally, *Tricarilda tareka* Gründel, 1997 (p. 142, pl. 4, figs. 51, 53─54) from the Middle Jurassic (late Bathonian) of Poland, is very similar to *Jurilda* sp. nov. Both species have opisthocyrt axial ribs on the shell surface intercepted by three spiral cords. However, the last teleoconch whorl of *T. tareka* is slightly more expanded than the spire and the shell outline is more gradate.

Occurrence. Lower Jurassic (late Toarcian); Northern England.

Family GORDENELLIDAE Gründel, 2000

Remarks. Schulbert & Nützel (2013) stated that gordenellids differ from mathildids in the ‘rather large size, slender to very slender shape, high number of whorls, early teleoconch whorls with mathildid ornament (three primary spiral ribs, middle and abapical spiral strongest and angulating whorl profile, numerous opisthocyrt axial ribs), and change of the ornament on mature teleoconch whorls (sometimes complete reduction)’. Here we follow Schulbert & Nützel (2013) for separation of these two families.

Genus TURRITELLOIDEA Walther, 1951

Type species. *Turritella opalina* Quenstedt, 1852, original designation, Toarcian to Aalenian, South Germany.

Occurrence. Lower Jurassic (Hettangian)-Upper Cretaceous; Germany, England, France, ?Luxemburg (Gründel & Nützel 2013).

Turritelloidea stepheni sp. nov.

(Fig. 4 R─S)

Derivation of name. Named for the second author’s father, Stephen Stanley-Little.

Type material. Holotype, YORYM: 2019.381; paratype, YORYM: 2019.382; two specimens preserved as external moulds.

Type locality. Ravenscar, North Yorkshire, England.

Type level. Late Toarcian (Blea Wyke Sandstone Formation, Yellow Sandstone Member), Cleveland Basin.

Diagnosis. Dextral, turriculate, slender shell; teleoconch up to nine whorls; earliest whorls with weakly nodular axial ribs; two adapical and abapical cords on earliest whorls, adapical cord stronger; spiral ornament dominant on mature whorls, 5-6 in number; opisthocyrt growth lines; shell base convex with spiral cords; aperture oval.

Description. Dextral, anomphalous, slender, turriculate and small-sized shell. The protoconch not preserved. Teleoconch has nine slightly convex whorls. Suture incised. Earliest teleoconch whorls have very weak, and slightly wide and opisthocyrt axial ribs with faint nodes abapically (Figure 4R). Two adapical and abapical spiral cords are situated near suture on earliest whorls; adapical cord stronger than abapical cord. Towards mature growth stages nodular axial ribs tend to disappear, and strongly opisthocyrt growth lines are visible. Spiral ornament dominant on mature whorls, comprising 4-5 thick and wide spiral cords intercalated by equally spaced, narrow spiral furrows. On last whorl 5-6 spiral cords present. Shell base strongly convex with six strong and regularly spaced broad spiral cords of equal strength, intercalated by narrower spiral furrows. Very fine prosocline growth lines intercept spiral cords on base. Aperture strongly oval with abapical channel.

Dimensions (mm). Holotype, YORYM: 2019.381: height, 7.82*; width, 2.34. Paratype, YORYM: 2019.382: height, 10.45*; width, 2.32*. (* = partial specimens).

Remarks. Following Gründel (2005) and Gründel & Nützel (2013), our specimens belong to the genus *Turritelloidea*. *T. opalina* Walther, 1951 (in Schulbert & Nützel 2013; p. 758, fig. 26A–D), from the Lower and Middle Jurassic (late Toarcian-early Aalenian) of Southern Germany, differs from *T. stepheni* sp. nov. in having a more developed spiral ornament on all teleoconch whorls, which forms a reticulate pattern with faint opisthocyrt axial threads, having small and pointed nodes at the crossing points, and in lacking the weakly nodular axial ribs on the earliest whorls. *Turritella* (*Mathilda*) *abbas* Hudleston, 1892 (p. 230, pl. 17, fig. 2), from the Middle Jurassic (Aalenian-Bathonian) of Bradford Abbas, Dorset, Southern England, differs from *Turritelloidea stepheni* sp. nov. in being slightly narrower and elongated, and in lacking axial elements on earliest whorls. *Turritella* (*Mathilda*) *strangulata* Hudleston, 1892 (p. 233, pl. 17, fig. 5), from the Middle Jurassic (Aalenian) of England, differs from *Turritelloidea stepheni* sp. nov. in having a deeply sulcated shell with a very oblique sutural angle.

Occurrence. Lower Jurassic (late Toarcian); Northern England.

Order ARCHITECTIBRANCHIA Haszprunar, 1985

Family TUBIFERIDAE Cossmann, 1895

Genus COSSMANNINA Gründel & Nützel, 2012

Type species. *Actaeonina* (*Ovactaeonina*) *abdominiformis* Schröder, 1995, Pliensbachian, North Germany.

Occurrence. Lower Jurassic (Pliensbachian)-Middle Jurassic (Callovian); Europe.

Cossmannina sp.

(Fig. 4 T─V)

Material. YORYM: 2019.383; one specimen preserved as an external mould.

Description. Fusiform, elongated, moderately high-spired and medium-sized shell; height 10.90 mm, width 5.32 mm. Partial protoconch heterostrophic. Teleoconch formed of five whorls; last whorl higher than spire. Sutural ramp lacking; suture incised. Upper portion of spire whorls broad, flattened and smooth, inclined 45º from sutures; outer face becomes straight. Flank of last whorl strongly convex. Shell surface with irregularly spaced, slightly prosocyrt to orthocline growth lines. Shell base slightly convex; aperture oval.

Remarks. Based on Gründel & Nützel (2012) our single specimen belongs to the genus *Cossmannina*. A very similar species to *Cossmannina* sp. is *Cossmannina*? *franconica* (Kuhn, 1935), from the Lower Jurassic (Pliensbachian) of Southern Germany. Both have the same general shell morphology and size, but *C*.? *franconica* has weak, narrow and irregularly spaced spiral furrows on the shell surface and base. *C. kalchreuthensis* (Gründel & Nützel, 1998) (p. 81 pl. 7, figs. 5─8 and Gründel 2007, p. 96, pl. 8, fig. 7 as *Ovactaeonina kalchreuthensis*; Nützel & Gründel 2015, p. 36, pl. 21, fig. I), from the Lower Jurassic (Pliensbachian) of Southern Germany, differs from *Cossmannina* sp. in being much smaller and having a more slender shell. *Cossmannina* sp. also resembles the type species *C. abdominiformis* (Schröder, 1995) (p. 68, pl. 12, figs 1–5, pl. 15, fig. 6 and Gründel 2007, p. 97, pl. 8, fig. 8 as *Ovactaeonina abdominiformis*; Nützel & Gründel 2015, p. 35, pl. 21 G), from the Lower Jurassic (Pliensbachian) of Northern Germany, but *C.*

abdominiformis is much smaller and has an egg-shaped and more bulbous shell, with the last whorl markedly more expanded than the spire. *C. sendelbachensis* (Kuhn, 1936) (p. 294, pl. 12, fig. 31, pl. 13, fig. 9 as *Pseudomelania sendelbachensis*; Gründel & Nützel, 1998, p. 80, pl. 6, figs 8–11 as *Ovactaeonina sendelbachensis*; Nützel & Gründel 2015, p. 36, pl. 21 J─L), from the Lower Jurassic (Pliensbachian) of Southern Germany, differs from *Cossmannina* sp. in being smaller, having a more slender and elongated shell, a higher spire with the rate of whorl expansion decreasing during ontogeny, and an aperture that is more elongated and rounded on its anterior part. *C. malzi* (Schroder, 1995) (p. 67, pl. 11, figs 16–20; Gründel & Nützel, 1998, p. 81, pl. 7, figs 2–4 as *Ovactaeonona malzi*; Nützel & Gründel 2015, p. 36, pl. 21 H), from the Lower Jurassic (Pliensbachian) of Southern Germany, differs from *Cossmannina* sp. in being much smaller, in having a more slender shell and a teleoconch consisting of three whorls.

Occurrence. Lower Jurassic (late Toarcian); Northern England.

Genus STRIACTAEONINA Cossmann, 1895

Type species. *Orthostoma avena* Terquem, 1855; Hettangian; Luxemburg.

Occurrence. Lower Jurassic-Upper Jurassic; Europe, South America.

Striactaeonina cf. *richterorum* Schulbert, Nützel & Gründel (in Schulbert & Nützel, 2013) (Fig. 4 W─Y)

2007c *Cylindrobullina* sp. 1 Gründel, p. 248, fig. 3E.

2013 *Striactaeonina richterorum* Schulbert, Nützel & Gründel in Schulbert & Nützel, p. 768, fig. 32E─G.

Material. YORYM: 2019.384 and YORYM: 2019.385; two specimens preserved as external moulds.

Description. Oval to cylindrical, slightly step-like or gradate, small-sized and moderately high-spired shell. Protoconch not preserved. Teleoconch consists of five whorls. Spire whorls strongly gradate in outline. Ramp broad, slightly convex and oblique; distinct spiral furrow delimits ramp from outer whorl faces. Ramp edge marked by distinct, wide, peripheral bulge. Outer face of spire whorls straight; outer face of last whorls slightly convex. Last whorl markedly more expanded than spire. The shell is smooth; very weak prosocline to prosocyrt growth lines visible on last whorl. Rounded transition between last whorl and base. Shell base ornamented by 5-6 regularly spaced spiral cords intercalated with equally developed spiral furrows. Apertural characters not preserved.

Dimensions (mm). YORYM : 2019.384: height, 2.38; width, 1.86. YORYM : 2019.385: height, 4.00, width, 1.84.

Remarks. Schulbert & Nützel (2013) described *Striactaeonina richterorum* from the early Aalenian of Southern Germany and considered *Cylindrobullina* sp. (in Gründel 2007, p. 248, fig. 3E), from the late Toarcian of Northern Germany as conspecific. Our two specimens are also very similar to *Striactaeonina richterorum* in Gründel (2007) and Schulbert & Nützel (2013), so we also consider them as being conspecific with *Striactaeonina richterorum*. However, the specimens described by Schulbert & Nützel (2013) have stronger spiral ornament on base and ramp is more vertical and more distinctly demarcated than the Yorkshire specimens, so we use the cf. designation for comparison. *Actaeonina* (*Striactaeonina*) *humeralis* Hudleston (1887, p. 472, pl. 42, figs. 20a, b), from the Dogger Formation (early Aalenian) of England is very similar to *Striactaeonina richterorum*, although the former species is smaller and has a broader and more convex ramp. *S. waltschewi* Schulbert & Nützel, 2013 (p. 766, fig. 32 H─J), from the Lower Jurassic (late Toarcian) of Southern Germany is similar to *S. richterorum*, however, *S. waltschewi* has a distinctly more elevated spire, a narrower ramp with rounded edge and two spiral furrows, and a very faint spiral striation on whorls flanks. *S. pseudmoorei* (Gründel & Buchholz, 1999) (p. 626, pl. 1, figs. 1─6 as *Actaeonina pseudmoorei*; Gründel, 2007, p. 93, pl. 7, fig. 14 as *Cylindrobullina pseudmoorei*; Gründel et al., 2011, p. 500, text-figure 13 A─H as *Cylindrobullina pseudmoorei;* Gründel & Nützel, 2012, p. 40, fig. 5 d─e), from the Lower Jurassic (late Pliensbachian) of Northern Germany and England, resembles *S. richterorum*, but *S. pseudmoorei* has a distinct peripheral spiral cord delimiting the ramp and the outer face of whorls,and this spiral cord is bounded on both sides by a spiral furrow.

Occurrence. Lower Jurassic (late Toarcian)-Middle Jurassic (early Aalenian); Northern and Southern Germany, England.

Striactaenonina elegans sp. nov.

(Fig. 5 A─E)

Derivation of name. Latin, adjective *elegans* = elegant; referring to the graceful appearance in shell shape and ornamentation.

Type material. Holotype, YORYM: 2019.386; paratype, YORYM: 2019.387; two specimens preserved as external moulds.

Type locality. Ravenscar, North Yorkshire, England.

Type level. Late Toarcian (Blea Wyke Sandstone Formation, Yellow Sandstone Member), Cleveland Basin.

Additional material. YORYM: 2019.388; one specimen preserved as an external mould.

Diagnosis. Oval, cylindrical shell; gradate spire; smooth, broad, oblique ramp delimited by a peripheral spiral bulge with a spiral furrow; shell surface ornamented by spiral furrows of unequal width;; shell base with 4-5 spiral furrows; aperture oval; concave columellar lip.

Description. Oval to cylindrical shape, gradate, small-sized shell. The protoconch and juvenile whorls not preserved. Teleoconch consists of four whorls; spire whorls with strongly gradate outline. Sutures incised. Ramp broad, smooth, slightly convex and oblique. Ramp edge marked by distinct, wide, peripheral spiral bulge. Outer face of spire whorls straight; outer face of last whorl faintly convex. Last whorl markedly more expanded than spire. Shell surface ornamented by irregularly spaced spiral furrows much narrower than interspaces between; opisthocline growth lines on the ramp of last whorl. Base convex and ornamented by 4-5 spiral cords. Aperture is partially preserved, oval, with thick and concave columellar lip.

Dimensions (mm). YORYM: 2019.386: height, 5.20; width, 2.69. YORYM: 2019.388: height, 4.65; width, 3.16. YORYM: 2019.387: height, 5.52; width, 3.29.

Remarks. Our specimens fit the diagnosis of the genus *Striactaeonina*, following Gründel and Nützel (2012) (see above). *S. richterorum* Schulbert & Nützel, 2013 (p. 768, fig. 32E─G; see above) differs from *S. elegans* sp. nov. in lacking the spiral cords on the shell surface, the weak spiral furrow and the opisthocline growth lines on the ramp. *S. waltschewi* Schulbert & Nützel, 2013 (p. 766, fig. 32 H─J), from the Lower Jurassic (late Toarcian) of Southern Germany, differs from *S. elegans* sp. nov. in having a distinctly more elevated spire, a narrower ramp and very faint spiral striation on the whorls flanks, rather than irregularly spaced spiral cords. *S. pseudmoorei* (Gründel & Buchholz, 1999) (p. 626, pl. 1, figs. 1─6 as *Actaeonina pseudmoorei*; Gründel, 2007, p. 93, pl. 7, fig. 14 as *Cylindrobullina pseudmoorei*; Gründel *et al*. 2011, p. 500, text-figure 13 A─H as *Cylindrobullina pseudmoorei*; Gründel & Nützel 2012, p. 40, fig. 5 d─e), from the Lower Jurassic (late Pliensbachian) of Northern Germany and England, lacks the spiral cords on the shell surface, has more distinct prosocyrt growth lines on last teleoconch whorl, and has a more prominent spiral bulge at the outer edge of the ramp. *C. dorsetensis* Gründel *et al*., 2011 (p. 500, text-figure 14A─E), from the Lower Jurassic (late Pliensbachian) of England, differs from *S. elegans* sp. nov. in having a more slender shell with an acute spire and more convex whorls, a narrower and oblique sutural ramp without edge, weaker spiral cords and furrows on the shell surface, and a high number of spiral cords on the base. Gründel *et al*. (2011) introduced a new combination for the type species *S. avena* (Terquem, 1855) and placed this into the genus *Cylindrobullina*. *C. avena* (Terquem, 1855) (p. 260, pl. 15, fig. 8, 8a as *Orthostoma avena*; Gründel *et al*., 2011, p. 500, text─figure 11E, F; Gründel & Nützel 2012, p. 40, fig. 5 c), from the Lower Jurassic (Hettangian-Sinemurian) of Luxemburg and England, differs from *S. elegans* sp. nov. in having a more slender shell, a more horizontal ramp demarked by a sharp edge, and smooth whorls. *Actaeonina (Striactaeonina) supraliasica* Cox (1965) (p. 173, pl. 29, figs. 4a, b, c), from the Lower Jurassic (Toarcian) of Kenya, differs *S. elegans* sp. nov. in being larger, having a more gradate spire with a steep and flattened ramp, a more cylindrycal last whorl, and regularly spaced spiral cords on the outer face of last whorl. *S. transatlantica* (Behrendsen, 1891) (p. 383, pl. 22, fig. 9 as *Actaeonina transatlantica*; Gründel 2011, p. 65, pl. 6, figs. 10─11; Ferrari 2017, p. 260, fig. 4.15─4.20), from the Lower Jurassic (Pliensbachian) of Argentina resembles *S. elegans* sp. nov. However, *S. transatlantica* is much larger, has a more horizontal sutural ramp, lacks the spiral peripheral bulge below the ramp, and has stronger and regularly spaced spiral cords on the shell surface. Finally, *S. atuelensis* Gründel, 2001 (p. 66, pl. 6, figs. 7─8), from the Lower Jurassic (early Pliensbachian) of Argentina is larger than *S. elegans* sp. nov. and has more convex whorls and lacks the peripheral spiral bulge.

Occurrence. Lower Jurassic (late Toarcian); Northern England.

Striactaenonina aff. *tenuistriata* (Hudleston, 1887)

(Fig. 5 F─I)

1887 *Actaeonina (Striactaeonina) tenuistriata* Hudleston, p. 471, pl. 42, figs. 18, 19.

Material. YORYM: 2019.389; one specimen preserved as an external mould.

Description. Oval to cylindrical shape, gradate and small-sized shell. Protoconch not preserved. Teleoconch consists of five whorls; spire whorls strongly gradate in outline and last whorl higher than the spire. Suture incised. Ramp broad, concave, smooth, oblique, and delimited by a bulge and a spiral furrow on mature whorls. A slightly adpressed bulge is visible; the second is stronger and peripheral, delimiting the ramp edge. Ramp edge marked by distinct, wide, peripheral spiral bulge. Outer face of spire whorls straight and ornamented with a faint spiral striation; outer face of last whorl faintly convex and ornamented by very thin and regularly spaced spiral cords intercalated by spiral furrows of same strength as spiral cords. Slightly prosocline growth lines on outer face of last whorl. Basal and apertural characters not preserved.

Dimensions (mm). YORYM: 2019.389: height, 6.68; width, 3.96.

Remarks. *Striactaeonina* aff. *tenuistriata* (Hudleston, 1887) is very similar in shell shape and ornamentation to *Actaeonina (Striactaeonina) tenuistriata* described by Hudleston (1887) from the Dogger Formation (early Aalenian) of England, but the latter species has spiral cords on last whorl and an ovate and elongated aperture. Because these characters are not preserved in our specimen, we cannot be entirely certain they are synonymous.

Striactaeonina aff. *tenuistriata* differs from *S. elegans* sp. nov. in being larger, having a concave ramp delimited by two spiral cords on mature whorls, and very thin and regularly spaced spiral cords on the outer face of last whorl. *S. richterorum* Schulbert & Nützel, 2013 (p. 768, fig. 32E—G; see above) and *S. waltschewi* Schulbert & Nützel, 2013 (p. 766, fig. 32 H—J) differ from *Striactaeonina* aff. *tenuistriata* in lacking both fine and regularly spaced spiral cords on the outer face of last whorl, and a concave ramp with the two adapical and peripheral spiral cords. *S. transatlantica* (Behrendsen, 1891) (p. 383, pl. 22, fig. 9 as *Actaeonina transatlantica*; Gründel 2011, p. 65, pl. 6, figs. 10—11; Ferrari 2017, p. 260, fig. 4.15—4.20) and *S. atuelensis* Gründel, 2001 (p. 66, pl. 6, figs. 7—8), both from the Lower Jurassic (early Pliensbachian) of Argentina, differ from *S.* aff. *tenuistriata* in having a straight and smooth ramp and stronger spiral cords and furrows on the shell surface.
Occurrence. Lower Jurassic (late Toarcian)-Middle Jurassic (Aalenian); Northern England.

Family CYLINDROBULLINIDAE Wenz, 1938
Genus CYLINDROBULLINA von Ammon, 1878

Type species. *Cylindrobullina fragilis* (Dunker, 1846); Lower Jurassic (Hettangian) of Northern Germany.
Remarks. Based on Gründel (2010) and Gründel & Nützel (2012) representatives of the genus *Cylindrobullina* have the following characters: cylindrical shell shape, the whorls embrace just below the subsutural ramp, the aperture is high and narrow, the spire is low and distinct, whorls are smooth or weakly ornamented with strengthened growth lines, spiral striae or spiral threads on base, growth lines on the flanks weakly prosocyrt and on the ramp directed backward and opisthocyrt, aperture very high, and the protoconch (although unknown from the type species) is heterostrophic.
Occurrence. Upper Triassic−Upper Jurassic; Europe, South America.

Cylindrobullina sp.
(Fig. 5 J—L)

Material. YORYM: 2019.390, YORYM: 2019.391, YORYM: 2019.392, YORYM: 2019.393, YORYM: 2019.394; five specimens preserved as external moulds.

Description. Oval to cylindrical shape, small-sized and moderately low-spired shell. Protoconch not preserved. Teleoconch consists of 5-6 strongly convex whorls. Spire slightly gradate in outline and last whorl higher than spire. Whorls are embrace just below the sutural ramp giving the ramp a very narrow appearance. Specimen YORYM: 2019.393 shows instead a very narrow sutural ramp. Suture impressed in deep concave furrow. Last whorl delimited by adapical spiral keel. Shell smooth, with fine and very weak prosocline to prosocyrt growth lines on last whorl. Shell base convex; aperture strongly oval with acute adapical channel and rounded basal lip.

Dimensions (mm). YORYM: 2019.392: height, 5.69*; width, 3.09. YORYM: 2019.390: height, 4.51*; width, 2.96. YORYM: 2019.393: height, 5.44*; width, 3.08. YORYM: 2019.394: height, 4.33; width, 2.98. * = partially preserved specimens.

Remarks. Based on the updated diagnosis of Gründel & Nützel, 2012, we assign our specimens to *Cylindrobullina*. Typical representatives of the genus have the whorls embrace just below the sutural ramp giving the ramp a very narrow appearance. However, specimen YORYM: 2019.393 has a very narrow sutural ramp; we consider this difference to be intraspecific variability. *Cylindrobullina* sp. differs from *C. arduenensis* (Piette, 1856) (in Gründel & Nützel 2012, p. 36, fig. 2), from the Lower Jurassic (Hettangian) of France, in being larger, having a more elevated spire and a narrower sutural ramp. Another similar species to *Cylindrobullina* sp. is *Actaeonina novozealandica* Bandel *et al*., 2000 (p. 101, pl. 10, figs. 8—10—12), from the Lower/Middle Jurassic of New Zealand. However, *Cylindrobullina* sp. is smaller, has a more slender shell with rounded sutural ramp grading into a narrow spiral groove. *C. avenoides* Haas, 1953 (p. 261, pl. 17, figs. 35, 36, 39—42, 46, 49—51, 58, 59), from the Upper Triassic of Peru, differs from *Cylindrobullina* sp. in having a more gradate shell outline with a broader sutural ramp, a steeper and higher spire, spiral cords on the shell surface, and an aperture with a better developed adapical channel. *C. vespertina* Haas, 1953 and *C. obesa* Haas, 1953 (p. 258, pl. 17, figs. 1—34; p. 264, pl. 17, figs. 54—57, 60—63), also from the Upper Triassic of Peru, differ from *C. convexa* sp. nov. in having a more gradate spire with a broader sutural ramp and a markedly more expanded last teleoconch whorl. The type species, *C. fragilis* Dunker, 1846 (p. 111, pl. 13, figs. 19a–b; Jaworski 1926, p. 205; Weaver 1931, p. 389), from the Lower Jurassic (Hettangian) of Germany and Argentina, is much larger than *Cylindrobullina* sp. and has a more gradate spire.

Occurrence. Lower Jurassic (late Toarcian); Northern England.

Family BULLINIDAE Gray, 1850

Genus SULCOACTAEON Cossmann, 1895

Type species. *Actaeonina striatosulcatus* Zittel & Goubert, 1861; Upper Jurassic (Oxfordian), France.

Remarks. Gründel (1997) established the new family Sulcoactaeonidae based on the genus *Sulcoactaeon* and placed the family within the superfamily Cylindrobullinoidea Wenz, 1947. The diagnosis of the genus *Sulcoactaeon* was recently updated by Kaim (2004), Kaim & Beisel (2005) and Gründel & Nützel (2012). Representatives of this genus have the following characters: slender to broadly oval shell. The protoconch is smooth and mostly coaxial with one to two visible whorls. The teleoconch whorls have a narrow and sometimes indistinct ramp with rounded abaxial edge as transition to the whorls flanks. The whorls are ornamented with spiral grooves, which may be frequent on the base. A spiral furrow demarcates the ramp. The growth lines are prosocyrt from the suture to the centre of the base. The aperture is narrowly oval.

Occurrence. Lower Jurassic (Pliensbachian)-Lower Cretaceous (Valanginian); Europe.

Sulcoactaeon sedgvici (Phillips, 1829)

(Fig. 5 M–R)

1829-35. *Auricula sedgvici*, Phillips. Geol. Yorks, part 1, pl. 11, fig. 33.

1850. *Acteon sedgvici* d'Orbigny. Prod., 1, p. 263.

1851. *Acteon sedgvici* Phillips. Morris and Lycett, Grt. Ool. Moll., part 1, p. 118, pl. 15, fig. 9.

1885. *Acteon sedgvici* Phillips. Hudleston, Geol. Mag., 1885, p. 252, pl. 5, fig. 4.
1887. *Actaeonina sedgvici* Phillips. Hudleston, p. 469, pl. 42, fig. 15.

Material. YORYM: 2019.395 (Fig. 5Q-R), YORYM: 2019.396 (Fig. 5M-O), YORYM: 2019.397 (Fig. 5P), YORYM: 2019.398, YORYM: 2019.399, YORYM: 2019.400, YORYM: 2019.401, YORYM: 2019.402, YORYM: 2019.403, YORYM: 2019.404, YORYM: 2019.405; eleven specimens preserved as external moulds.

Description. Globose, broadly oval, small-sized and low-spired shell. Protoconch not preserved. Teleoconch formed of 4-5 whorls; last whorl higher than spire. Spire more or less gradate; outer face of spire whorls slightly concave (see Figure 5M). Sutural ramp narrow and horizontal and suture impressed in deep spiral furrow. Last teleoconch whorl strongly convex and ornamented by more or less regularly spaced spiral grooves; spiral grooves located below the middle of last whorl slightly broader than the rest. Spiral grooves absent from juvenile whorls. Shell base strongly convex and also ornamented by spiral grooves; the former are thinner and more crowded than on outer face of whorls. Aperture strongly oval with acute adapical channel and strongly rounded basal lip. Very weak growth lines intercept spiral grooves on base.

Dimensions (mm). Table 4.

Remarks. Our specimens are conspecific with *Actaeon sedgvici* Phillips, 1829, also from the late Toarcian and Aalenian-Bajocian of England. Gründel, Nützel & Schulbert in Gründel (2007) reported the species *Sulcoactaeon laevis* from the late Toarcian?-early Aalenian of Northern Germany. However, this species differs considerably from true representatives of *Sulcoactaeon*. *Sulcoactaeon sendelbachensis* Nützel & Gründel, 2015 (p. 37, fig. 4; Gründel & Nützel 1998, p. 82, pl. 7, figs. 11─12 as *Sulcoactaeon*? sp.), from the Lower Jurassic (late Pliensbachian) of Southern Germany, has more convex whorls, a slightly more elevated spire and a less expanded last whorl than *S. sedgvici*. *Ragactaeon spiralosulcata* Gründel, 1997 (p. 94, pl. 7, figs. 18─20), from the Lower Jurassic (late Pliensbachian) of Germany, differs considerably from *S. sedgvici* in having a strongly more developed sutural ramp with a stronger adapical spiral furrow, and weaker and indistinct spiral furrows on the flank of whorls. *S. bojarkensis* Kaim & Biesel, 2005 (p. 55, fig. 13), from the Upper Jurassic (early Kimmeridgian) of Russia, differs from *S. sedgvici* in having more convex whorls, an indistinct sutural ramp, whorl ornamentation consisting of pitted and weaker spiral cords, and a slightly more oval aperture with an acute adapical channel. *S. timanicus* Kaim & Biesel, 2005 (p. 54, fig. 12), also from the Upper Jurassic of Russia, has a more spindle-like and slender shell than *S. sedgvici* a weakly angulated sutural ramp, and prosocline growth lines that thicken into narrow riblets when crossing the ramp. *S. polonicus* Kaim, 2004 (p. 153, fig. 131) from the Middle Jurassic (Bathonian) of Poland, has a broader sutural ramp, a more slender shell, and a teleoconch starting with two distinct adapical spiral cords.

Occurrence. Lower Jurassic (late Toarcian)-Middle Jurassic (Bajocian); Northern England.

EARLY TOARCIAN EXTINCTION AND RECOVERY OF GASTROPOD FAUNAS IN THE CLEVELAND BASIN

Gastropods formed only a small component of the molluscan diversity in the pre-extinction faunas of the late Pliensbachian and early Toarcian in the Cleveland Basin (e.g. Harries & Little 1999), with seven species in six families (Eucyclidae, Gosseletinidae, Coelodiscidae, Tubiferidae, Zygopleuridae and Ptychomphalidae) recorded in the late Pliensbachian (*Margaritatus* to *Spinatum* Zones) and early Toarcian *Tenuicostatum* Zone [Ferrari et al. (2020, table 2)]. The onset of laminated black shale facies at the top of the early Toarcian *Tenuicostatum* Zone resulted in the disappearance of all gastropods (and many other taxa, Harries and Little 1999) in the Cleveland Basin, and gastropods were absent in the basin until the upper part of the early Toarcian *Falciferum* Zone, where there is single occurrence of the caenogastropod species *Cryptaulax* cf. *slatteri* (Tate, 1870). In the middle Toarcian *Bifrons* and *Variabilis* Zones, with the amelioration of benthic oxygen conditions, the gastropod fauna increased to four species in three families (Procerithiidae, Aporrhaidae and Cylindrobullinidae) (Figure 6A). The gastropod diversity then increased substantially to 18 species in 11 families in the Blea Wyke Sandstone Formation of the late Toarcian (*Thoarsense* and *Levesquei* Zones) [Ferrari et al. (2020, table 2), Figure 6A], where they became a much more dominant component of the contemporary molluscan faunas, both numerically and in diversity, compared to those of the late Pliensbachian and early

Toarcian *Tenuicostatum* Zone (JWA, unpublished data). In the Dogger Formation of the early Aalenian (*Opalinum*? Zone) gastropod diversity increased again to 44 species in 17 families [Ferrari et al. (2020, table 2), Figure 6A].

In the Cleveland Basin the impact of the early Toarcian extinction event on the gastropod faunas resulted in the almost complete replacement of species. It also had important implications for higher taxa, because the late Pliensbachian species *Sisenna* cf. *pinguis* (Deslongchamps, 1849) and *Angulomphalus expansus* (J. Sowerby, 1821) were amongst the last representatives of their families (Gosseletinidae and Ptychomphalidae respectively) globally. The post-extinction gastropod faunas of the middle and late Toarcian contained some of the first representatives of higher taxa that would later become common elements in Middle Jurassic gastropod assemblages: *Pietteia arenosa* (Hudleston 1884) and *Pietteia unicarinata* (Hudleston 1884) (family Aporrhaidae), *Procerithium armatum* (Goldfuss 1843), *Procerithium quadrilineatum* (Römer, 1836) (Family Procerithiidae), and *Turritelloidea stepheni* sp. nov. and *Turritelloidea quadrivittata* (Phillips, 1829) (Family Gordenellidae) being good examples. However, only four species (*Pietteia unicarinata*, *Globularia* cf. *canina*, *Sulcoactaeon sedgvici*, and *Striactaenonina* aff. *tenuistriata*) are shared between the late Toarcian and Aalenian Dogger Formation faunas in the Cleveland Basin [Ferrari et al. (2020, table 2)]. The Dogger Formation contains typical representatives of European Middle Jurassic gastropod assemblages (e.g. the families Pseudomelaniidae, Ataphridae, Nerineidae, Neritidae, Neritopsidae, Trochotomidae), and also typical of Middle Jurassic gastropod assemblages, has a greater diversity of gastropods at all taxonomic levels, compared to Lower Jurassic faunas (Figure 6B). There may be a facies control on the pattern of gastropod recovery from the early Toarcian extinction event in the Cleveland Basin. The late Pliensbachian sedimentary rocks are very heterogeneous, with oolitic ironstones, fine sandstones and siltstones (Cleveland Ironstone Formation), and were deposited in shallow water settings (Hesselbo 2008), whereas the early and middle Toarcian rocks are fine grained (Whitby Mudstone Formation; Figure 2), representing transgressive, deeper water facies (Hesselbo 2008). These fine grained facies were generally not optimum for gastropod diversity in the Lower Jurassic. Post-extinction diversity only increased in the Blea Wyke Sandstone Formation, three ammonite zones after the extinction event, when shallower-water, coarser-grained sediments started to be deposited in the Cleveland Basin, and this facies tends to have greater gastropod diversity in the Jurassic. The facies changed again with the Aalenian Dogger Formation, with the deposition of oolitic sandy ironstones; oolitic facies of the Middle Jurassic tend to have high diversity gastropod faunas. Interestingly, vetigastopods were only present the Cleveland Basin during the late Pliensbachian to Aalenian interval when oolitic ironstones were being deposited, perhaps further indicating a facies control on the gastropod faunas (Figure 6B).

LATE TOARCIAN WESTERN EUROPEAN GASTROPOD FAUNAS

Comparing the late Toarcian gastropod fauna of the Cleveland Basin with those in the marine deposits of Southern Germany (Franconia Basin; Schulbert & Nützel, 2013), Northern Germany (Jurensismergel Formation, North German Basin; Gründel, 2007) and Southern France (Causses Basin; Gatto *et al*., 2015) allows us to analyse the palaeobiographic distribution of gastropods in Western Europe during this time period, showing that there are some major differences [Figure 7, Ferrari et al. (2020, table 3)]. The Cleveland Basin late Toarcian gastropod fauna is well represented by several caenogastropod and heterobranchid families, including the Procerithiidae, Coelodiscidae, Aporrhaidae, Ampullinidae, Zygopleuridae, Palaeorissoinidae, Mathildidae, Gordenellidae, Tubiferidae, Cylindrobullinidae and Bullinidae; two families, the Zygopleuridae and Ampullinidae, only occur in the Cleveland Basin during this time interval (Fig. 7 C). In contrast, members of the orders Vetigastropoda and Cycloneritimorpha, and the families Discohelicidae, Iravadiidae, Lamelliphoridae, Cryptaulicidae, Strombidae, Maturifusidae, Tofanellidae, Ebalidae and Cornirostridae, typical of the Jurensismergel Formation, and Franconia and Causses Basins, are missing from the Cleveland Basin late Toarcian faunas [Fig. 7 C, Ferrari et al. (2020, table 3)]. The sediments of Jurensismergel Formation and in the Franconia Basin represent typical marine epicontinental deposits of mudstones and marls deposited in calm conditions below storm wave base (e.g., Etter 1995; in Schulbert & Nützel, 2013). These resulted in soft bottom conditions with soupy substrates and variable oxygen availability (fully aerobic to dysaerobic), contrasting strongly with the sandy sediments of the Blea Wyke Sandstone Formation being deposited above storm wave-base at the same time in the Cleveland Basin. This suggests a facies control on the composition of contemporary gastropod faunas between these regions. The low diversity in the late Toarcian gastropod faunas from the Causses area (Figure 7 A, B) may have been due to the restricted nature of the Causses Basin, which was confined largely by land masses and open only towards the central part of western Tethys Ocean. The geographic isolation and marginal location of the Causses Basin probably restricted faunal exchange with the Western European epicontinental seas, preventing a rapid recovery after the early Toarcian extinction event. According to Fürsich *et al*. (2001), the changes in the macrobenthic associations recorded in the Causses succession after the early Toarcian anoxic event were related to changes in oxygenation and substrate consistency. In the lower part of the sequence the low diversity reflected oxygen fluctuations, whereas the extremely soupy substrate resulting from the activity of burrowing organisms was the main controlling factor during the late Toarcian time period. Gastropods from the central region of the Western Tethys were probably unable to settle and colonize the Causses area at this time because of differences in environment (Gatto *et al*. 2015).

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: http://zoobank.org/References/XXXXXXXXX

Data for this study are available in the Dryad Digital Repository: https://datadryad.org/stash/share/nhYDj6xiGWcDrEia0J9vssLmIghbupAPoEdH9g98jYQ

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CAPTIONS

FIG. 1. A. Map of England showing Lower Jurassic outcrops, sedimentary basins and location of the Ravenscar section. B. Detailed geological map of the Ravenscar area, North Yorkshire.

FIG. 2. Log of the Ravenscar section from the top of the Alum Shale Member to the Dogger Formation, showing sampling horizons.

FIG. 3. **A**–**E**, *Coelodiscus minutus* (Schübler *in* Zieten, 1833). A–E, YORYM: 2019.315., A–B, apical views; C, apical view detail; D–E protoconch and earliest whorls details; specimen from sample horizon ys-d.400. **F**–**L**, *Procerithium quadrilineatum* (Römer, 1836). F-H, YORYM: 2019.320., F-G, lateral and apertural views, H, apertural detail; specimen from sample horizon ys-d.400. I–L, YORYM: 2019.319, I–J, lateral views, K–L, juvenile teleoconch details; specimen from sample horizon ys-d.100. **M**–**R**, *Katosira*? *bicarinata* sp. nov. M–N, YORYM: 2019.344, holotype, lateral and apertural views; specimen from sample horizon ys-d.400. O, YORYM: 2019.346, lateral view; specimen from sample horizon ys-d.400. P, YORYM: 2019.347, lateral view; specimen from sample horizon ys-d.400. Q–R, YORYM: 2019.345, paratype, lateral views; specimen from sample horizon ys-d.500. **S**–**U**, *Pseudokatosira undulata* (Benz, 1830 in von Zieten). S, YORYM: 2019.354, fragmentary specimen in lateral view, last whorl and basal details are shown; specimen from sample horizon ys-d.500. T–U, YORYM: 2019.353, lateral views; specimen from sample horizon ys-d.400. **V**–**X**, *Palaeorissoina* aff. *acuminata* (Gründel, 1999b). V–W, YORYM: 2019.358, lateral and apertural views; specimen from sample horizon ys-d.200. X, YORYM: 2019.359, lateral view; specimen from sample horizon ys-d.200. Scale bars represent 500 mm (A, B, D, E, O, P, V, W, X); 1 mm (F, G, H, I, J, K, M, N, Q, R, S, T, U); 100 mm (C); 200 mm (L).

FIG. 4. **A**–**L**, *Pietteia unicarinata* (Hudleston, 1884). A–C, YORYM: 2019.360. A, C, lateral views; B, protoconch and early teleoconch details; specimen from sample horizon ys-d.200. D, YORYM: 2019.362, lateral and apertural views; specimen from sample

horizon ys-d.200. E, YORYM: 2019.361, lateral view; specimen from sample horizon ys-d.100. F, YORYM: 2019.369; specimen from sample horizon ys-d.400. G–H, YORYM: 2019.376, extension of the outer lip detail; specimen from sample horizon ys-d.700. I–J, YORYM 2019.377, lateral views and apex in oblique view; specimen not in-situ. K–L, YORYM: 2019.364, lateral and basal views; specimen from sample horizon ys-d.700. **M–N,** *Globularia* cf. *canina* (Hudleston, 1882), YORYM: 2019.378, lateral and apical views; specimen not in-situ. **O**–**P**, *Tricarilda*? sp., YORYM: 2019.379, lateral views; specimen from sample horizon ys-d.200. **Q**, *Jurilda* sp., YORYM: 2019.380, lateral view; specimen from sample horizon ys-d.400. **R**–**S**, *Turritelloidea stepheni* sp. nov., YORYM: 2019.381, holotype, lateral and apertural views; specimen from sample horizon ys-d.400. **T**–**V**, *Cossmannina* sp., YORYM: 2019.383. T–U, lateral views; V, apertural view; specimen from sample horizon ys-d.600. **W**–**Y**, *Striactaeonina* cf. *richterorum* Schulbert & Nützel, 2013. W, YORYM: 2019.384, lateral view; specimen from sample horizon ys-d.400. X–Y, YORYM: 2019.385, lateral views; specimen from sample horizon ys-d.300. Scale bars represent 1 mm (A, C, D, E, G, H, K, L, M, N, Q, R, S); 5 mm (I, J); 500 μm (F, O, P, W, X, Y); 200 μm (B, T, U, V).

FIG. 5. **A**–**E,** *Striactaeonina elegans* sp. nov. A–C, YORYM: 2019.386, holotype, lateral views; specimen from sample horizon ys-d.500. D–E, YORYM: 2019.388, lateral views; specimen from sample horizon ys-d.200. **F**–**I,** *Striactaenonina* aff. *tenuistriata* (Hudleston, 1887), YORYM: 2019.389; F–G, lateral views; H, spire whorls detail; I, last whorl ornament detail; specimen from sample horizon ys-d.700. **J**–**L**, *Cylindrobullina* sp., J, YORYM: 2019.390, apical view; specimen from sample horizon ys-d.400. K–L, YORYM: 2019.391, apical and lateral views; specimen from sample horizon ys-d.200. **M**–**R**, *Sulcoactaeon sedgvici* (Phillips, 1829), **M**–**O**, YORYM: 2019.396, lateral views; specimen from sample horizon ys-d.100. **P**, YORYM: 2019.397, lateral view; specimen from sample horizon ys-d.200. **Q**–**R**, YORYM: 2019.395, lateral and apertural views; specimen from sample horizon ys-d.400. Scale bars represent 500 μm (A, B, C, D, E, H, I, J, K, L, O, P, Q, R); 1 mm (F, G, M, N).

FIG. 6. Effect of the early Toarcian extinction event on gastropod faunas of the Cleveland Basin. **A.** Numbers of gastropod species (Species), genera (Genera) and families (Family) for the late Pliensbachian to the Aalenian interval in four time bins. **B**. Relative percentage of gastropod orders for the same time bins.

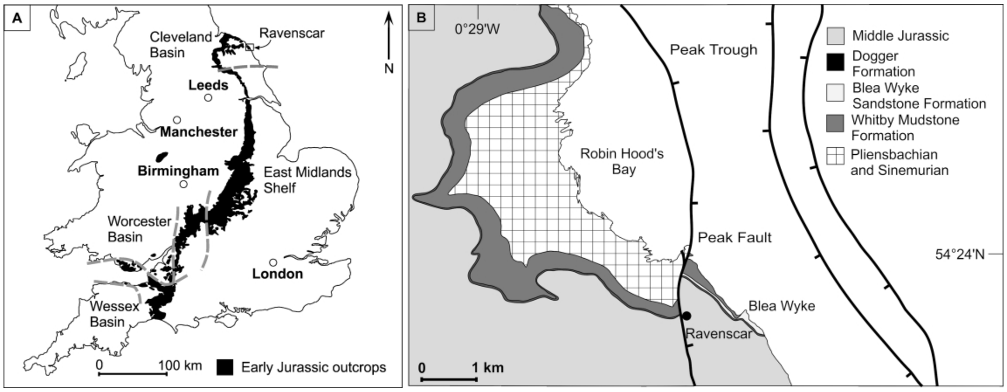
FIG. 7. **A**–**C**, Taxomonic comparison of Late Toarcian gastropods from the Cleveland Basin, Franconia Basin (Southern Germany), Jurensismergel Formation, North German Basin (Northern Germany) and Causses Basin (Southern France). **A**. Pie chart of relative proportion of species in the four areas. **B**. Numbers of species, genera and families in the four areas. **C**. Family composition of gastropod species in the four areas.

TABLE 1. Dimensions (mm) of *Procerithium quadrilineatum* (Römer, 1836). * = partial specimens.

TABLE 2. Dimensions (mm) of *Katosira*? *bicarinata* sp. nov. * = partial specimens.

TABLE 3. Dimensions (mm) of *Pietteia unicarinata* (Hudleston, 1884). * = partial specimens.

TABLE 4. Dimensions (mm) of *Sulcoactaeon sedgvici* (Phillips, 1829). * = partial specimens.



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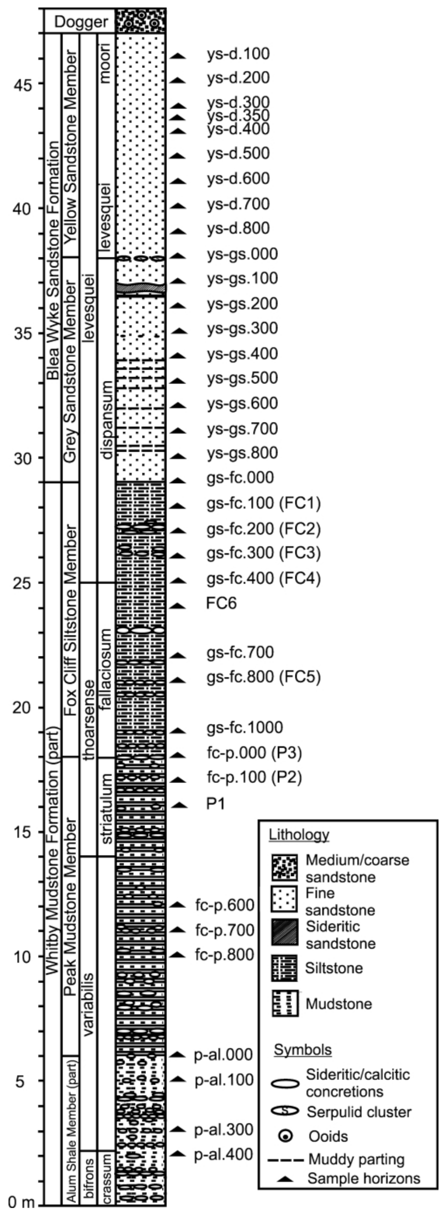

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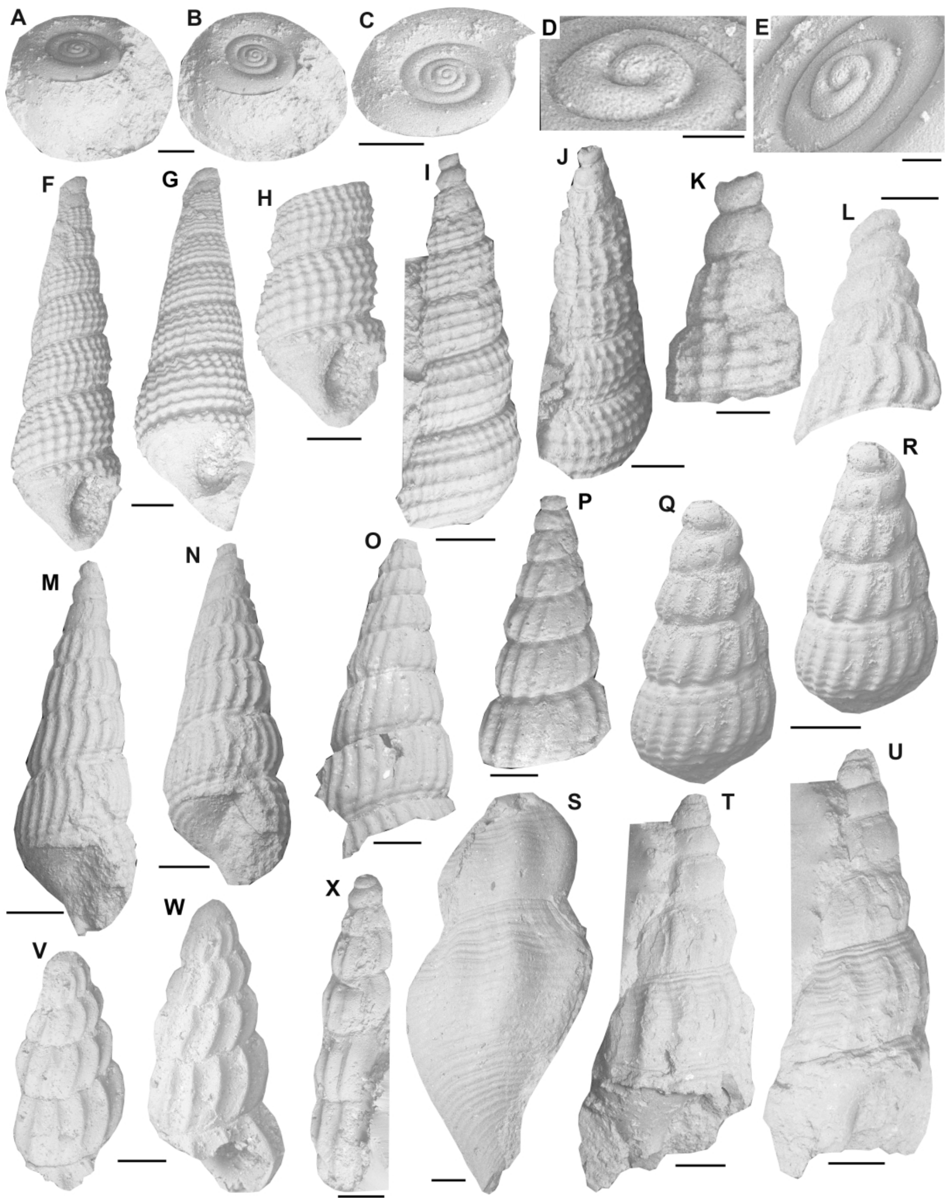

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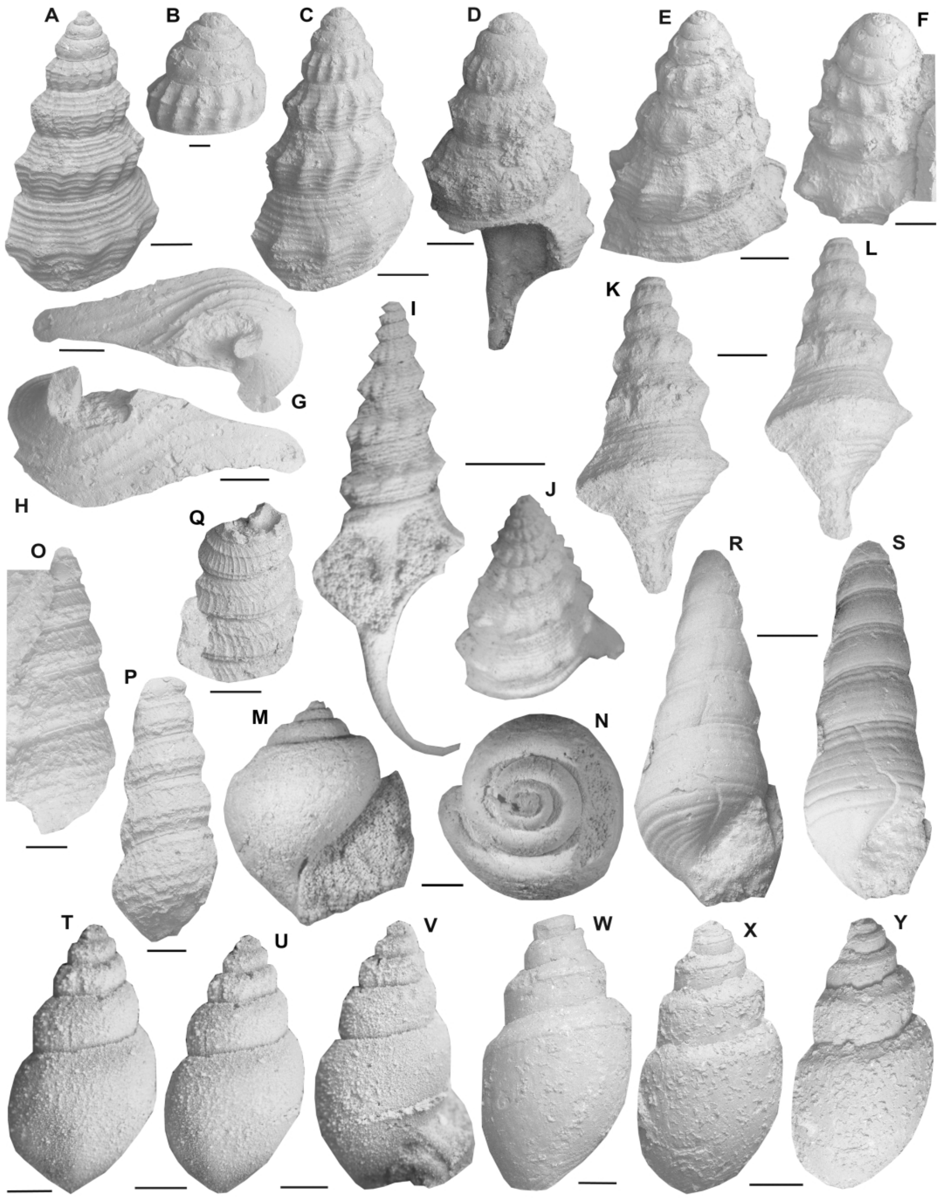

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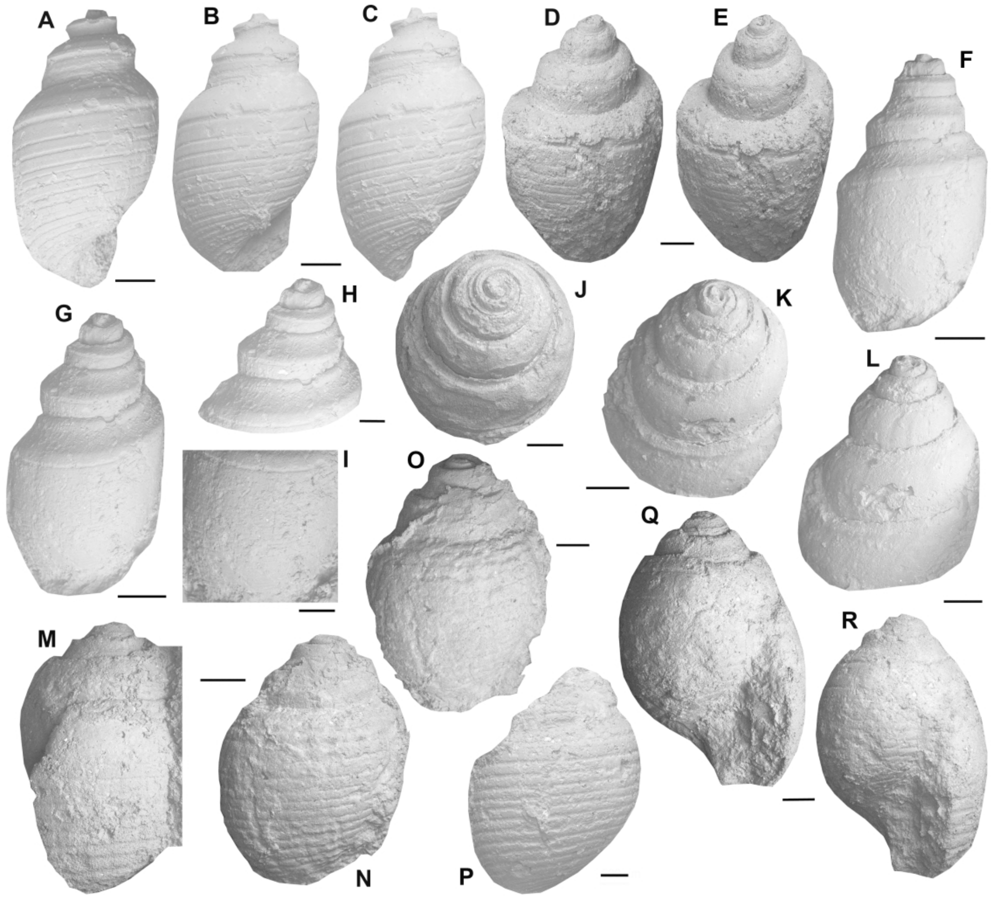
represent 1 mm (A, C, D, E, G, H, K, L, M, N, Q, R, S); 5 mm (I, J); 500 □m (F, O, P, W, X, Y); 200 □m (B, T, U, V).



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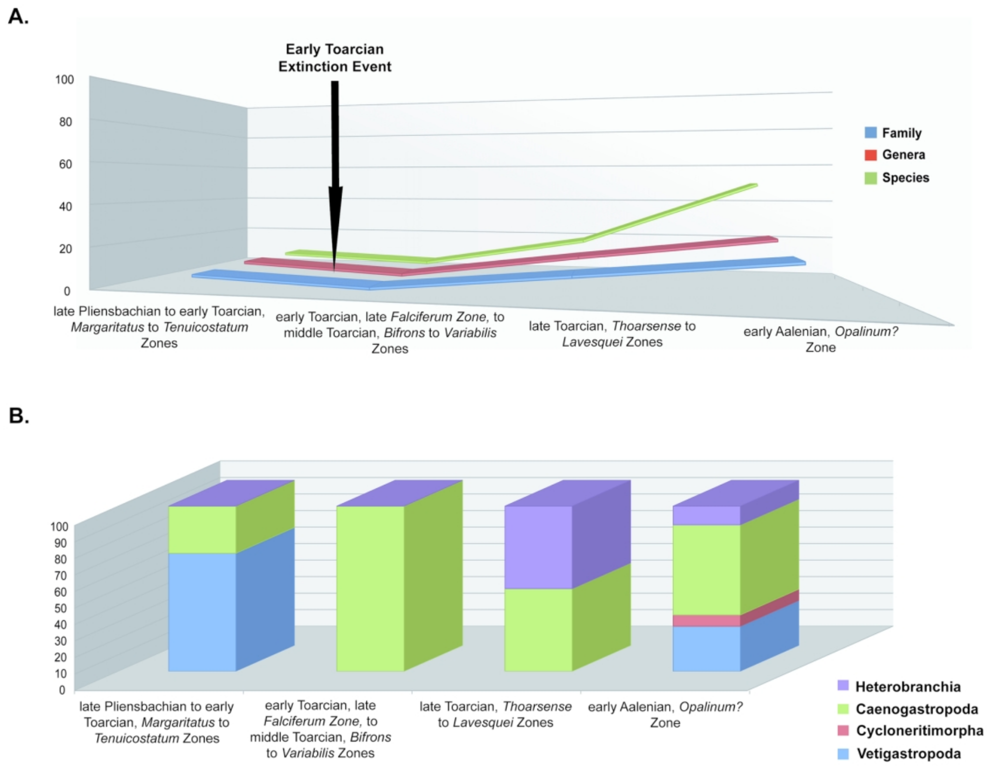

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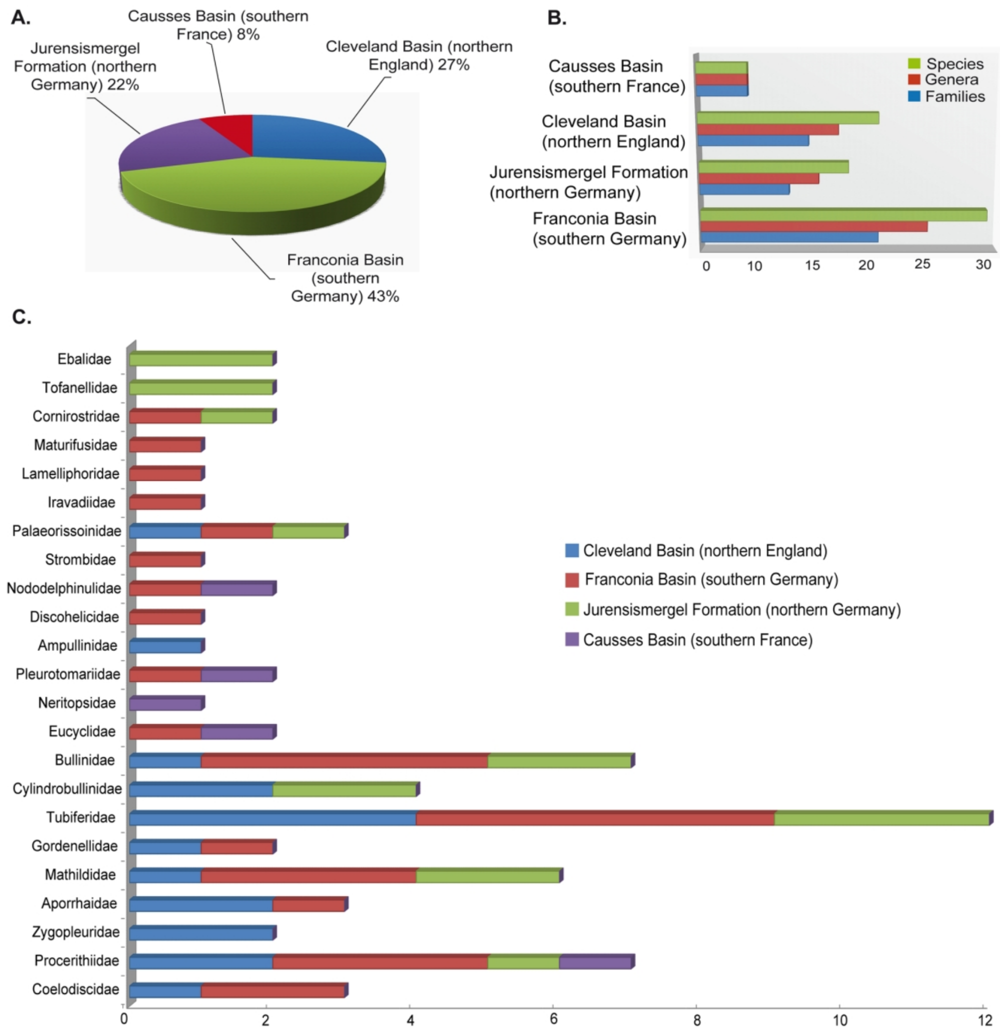
165x127mm (300 x 300 DPI)



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165x171mm (300 x 300 DPI)

Procerithium quadrilineatum (Römer, 1836)		
Specimen	height (mm)	width (mm)
YORYM : 2019.317	7.00	1.90
YORYM : 2019.318	1.81	0.74
YORYM : 2019.319	6.51	2.17
YORYM : 2019.337	4.00*	1.89
YORYM : 2019.338	4.64*	1.67*
YORYM : 2019.339	0.92*	1.13
YORYM : 2019.320	8.14	2.13
YORYM : 2019.321	4.88	2.11
YORYM : 2019.341	7.53	2.69
YORYM : 2019.342	8.32	2.41
YORYM : 2019.343	5.98*	3.16
YORYM : 2019.322	6.94*	3.97
YORYM : 2019.323	7.44*	2.09
YORYM : 2019.340	15.29*	5.25

Katosira? *bicarinata* sp. nov.			
Specimen	Type	height (mm)	width (mm)
YORYM : 2019.350	–	3.72*	1.72
YORYM : 2019.344	Holotype	7.11	2.51
YORYM : 2019.346	–	4.54*	1.76
YORYM : 2019.345	Paratype	4.61*	2.06
YORYM : 2019.349	–	4.71	2.02
YORYM : 2019.351	–	6.62	2.10
YORYM : 2019.348	–	4.45*	2.03
YORYM : 2019.347	–	4.26*	1.73

Pietteia unicarinata (Hudleston, 1884)		
Specimen	height (mm)	width (mm)
YORYM : 2019.364	7.62*	3.49
YORYM : 2019.365	5.70	2.43
YORYM : 2019.366	4.48*	2.41
YORYM : 2019.362	6.79	2.59
YORYM : 2019.360	5.68*	3.05
YORYM : 2019.367	4.52*	2.8*
YORYM : 2019.368	7.03*	4.18*
YORYM : 2019.369	3.71*	1.61*
YORYM : 2019.370	2.73*	2*
YORYM : 2019.371	5.98*	3.79*
YORYM : 2019.377	24.81	7.94

Sulcoactaeon sedgvici (Phillips, 1829)		
Specimen	height (mm)	width (mm)
YORYM : 2019.400	3.04*	2.13
YORYM : 2019.401	2.98	2.23
YORYM : 2019.397	3.35*	1.93*
YORYM : 2019.398	3.63*	2.87
YORYM : 2019.402	4.04*	2.65
YORYM : 2019.395	4.76	3.36
YORYM : 2019.396	4.79	3.57
YORYM : 2019.403	3.72	2.40*
YORYM : 2019.404	3.31	2.17*
YORYM : 2019.405	3.95*	3.12