Homeomorphic gastropods from the Silurian of Norway, Estonia and Bohemia

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Redescription of the gastropod *Euomphalus undiferus* Schmidt, 1858 from the Upper Llandovery Rumba Formation of Estonia requires reinvestigation of the hitherto monotypic genus *Kiaeromphalus* Peel & Yochelson, 1976, originally described from the Rytteråker Formation of the Oslo Region. The Estonian *K. undiferus* and the Norwegian type species occur in similar depositional facies of Early Silurian age within the *sedgwickii* Graptolite Zone. The redescribed type specimen of *Horologium kokeni* Perner, 1907 from the late Silurian (Ludlow) of Bohemia shows strong morphological convergence with the two Baltic species, but *Kiaeromphalus* is distinguished by its lower rate of whorl expansion and less oblique aperture. Both genera were adapted to a sessile life, possibly on a soft substratum.

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Introduction

In 1976, Peel & Yochelson reviewed Early Silurian (Llandovery) gastropods from the Oslo Region and proposed two new genera, *Kiaeromphalus* and *Kjerulfonema*, which they named after the prominent Norwegian palaeontologists Johan Kiær and Theodor Kjerulf. The high-spired, spirally ribbed, *Kjerulfonema quinquecincta* (Kjerulf, 1865) was considered to be congeneric with *Turritella cancellata* Sowerby *in* Murchison, 1839 from the Llandovery of the United Kingdom, but Peel & Yochelson (1976) did not assign any other described species to the large, low-spired *Kiaeromphalus.*

A review of Siluro-Devonian collections from Romania, subsequently described by Horný & Iordan (1994) along with Dr Radvan J. Horný (National Museum, Prague), raised a suspicion that *Kiaeromphalus* might be a junior synonym of *Horologium* Perner, 1907, originally described from the Upper Silurian of Bohemia. Unfortunately, the Romanian specimen, while assigned to the type species of *Horologium,* was poorly preserved and the issue could not be resolved. Subsequent ongoing investigation of Silurian gastropod faunas from Estonia revealed Llandovery specimens closely related to *Kiaeromphalus kristianiensis* Peel & Yochelson, 1976, which proved to belong to the previously *non*-figured species *Euomphalus undiferus* Schmidt, 1858. This discovery stimulated recent re-examination of the holotype of *Horologium kokeni* Perner, 1907 in Prague to elucidate its relationship to *Kiaeromphalus.*

In this paper we redescribe *Horologium kokeni* and *Euomphalus undiferus*, comparing both with *K. kristianiensis*. *Horologium* Perner, 1907 and *Kiaeromphalus* Peel & Yochelson, 1976 are recognized as separate, homeomorphic, genera; Schmidt's (1858) species from Estonia is ascribed to the latter genus. Thus, *Kiaeromphalus* occurs from southern Norway to Estonia in the Lower Silurian rocks, although it remains unreported from the Silurian of Sweden. The single specimen of the type species of *Horologium* from Bohemia and the single specimen from Romania assigned to this species are of late Silurian age.

Kiaeromphalus in Estonia and Norway

Schmidt (1858) described Ordovician and Silurian fossils from Estonia, but failed to figure any of his material. Some 48 species of gastropods including 7 new taxa were treated, most of which were originally described by d'Eichwald (1840, 1856) and later illustrated by the same author (d'Eichwald 1860). A few species were subsequently also redescribed and figured by Koken (1889) and Koken & Perner (1925). The species *Euomphalus undiferus* Schmidt, 1858 discussed in this paper has been mentioned in the literature (see synonymy list), but neither figured nor revised. Only a few specimens were held in the Museum of Geology, University of Tartu, Estonia (TUG) along with the type specimen. The search for additional material in the collections in the Institute of Geology, Tallinn, the Museum of Palaeontology and Stratigraphy, University of St. Petersburg, the Museum of the St. Petersburg Mining Institute and the Central Scientific Research Geological Exploration Museum, St. Petersburg, proved negative. However, recently collected topotype material led to close comparison with the type material of *Kiaeromphalus* from the Lower Silurian of Norway, and now with *Horologium kokeni.*

The Estonian species is from the upper part of the Upper

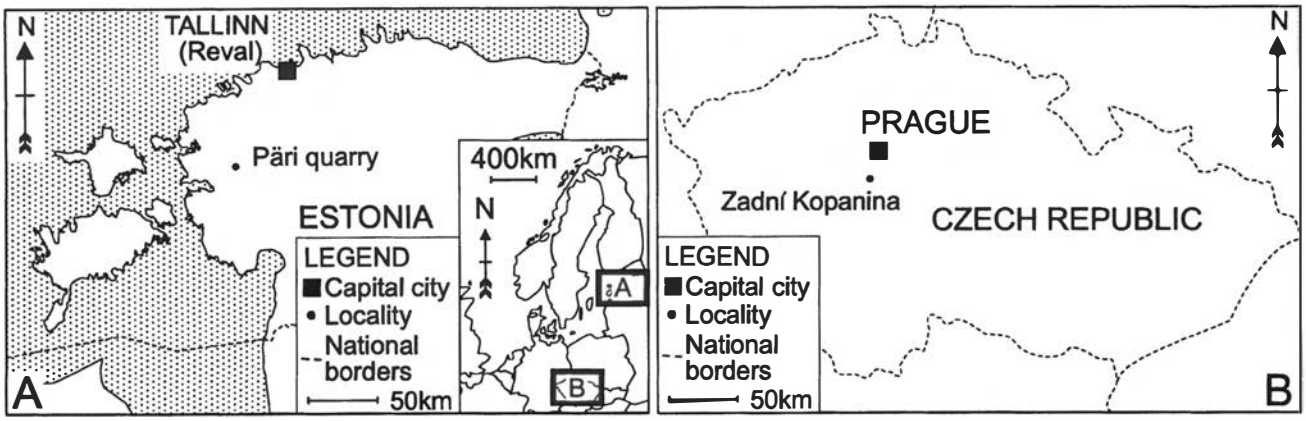

Fig. 1. Locality map of Estonia (A) and Bohemia, Czech Republic (B).

Llandovery (Aeronian) Rumba Formation at the Päri quarry, earlier named Kattentack, in southwest Estonia (Figs. 1, 2). Schmidt (1858) also mentioned the locality Jõgisoo, earlier called Jöggis, representing the same unit; today that locality is no longer accessible and material from it has not been identified. In regional terms the level corresponds to the lower part of the Adavere Regional Stage (H) for which Päri is the type section, and the formation corresponds closely to the *sedgwickii* Graptolite Zone. The unit is about 20 m and is developed in central and southern Estonia and northern Latvia as a transgressive biomicritic limestone (wackstone or skeletal packstone) with intercalations of clay (Klaamann 1984; Bassett et al. 1989; Kaljo & Einasto 1990, Nestor *in* Raukas & Teedumäe 1997). Abundant specimens of *Pentamerus* occur as scattered shells or tempestitic accumulations.

Kiaeromphalus kristianiensis Peel & Yochelson, 1976 is found in the approximately 115 m thick Rytteråker Formation in Norway, formerly the Pentamerus Limestone (*etasje* 7a–b), in the central Oslo area of the Oslo Region and possibly in the Holmestrand area just south of Oslo. The unit falls within the *sedgwickii* to *crispus* graptolite zones (Worsley et al. 1983), a slightly longer range than that of the Rumba Formation in Estonia (Fig. 2).

The type series of *Kiaeromphalus* was collected and labelled by Johan Kiær and his associates between 1902 and 1907, prior to the published stratigraphical scheme of the Silurian succession in the Oslo Region (Kiær 1908). Peel & Yochelson (1976) pointed out that the labelling of the samples collected in this period reflect Kiær's changing views during the field seasons regarding the position of the 7a–7b levels. They therefore concluded that their new genus extended through most of *etasje* 7. However, in his synopsis on the Silurian stratigraphy in the Oslo Region,

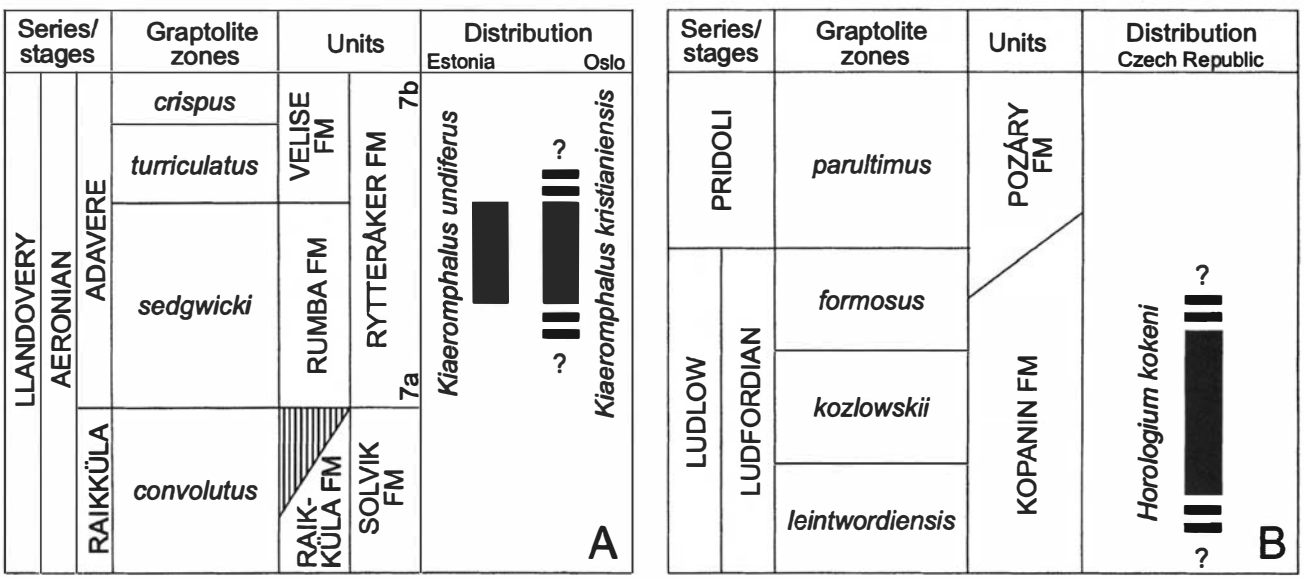

Fig. 2. Stratigraphical units and biostratigraphical distribution of *Kiaeromphalus* species in the Llandovery Series in Baltica (A) and *Horologium* in the Ludlow of Bohemia (B).

Kiær (1908, p. 352) lists a 'large, beautiful' *Pleurotomaria* from the upper part of 7a and 7bα in the Oslo–Asker district along with a *Cyclonema* sp. In the lower part of 7a he lists a large *Bellerophon* sp., whereas no gastropod fossils are listed from the 7b part of the sequence in the Oslo–Asker district. Assuming that the material collected by Kiær was the basis for his faunal lists, it is possible that the *Pleurotomaria* species represents the *Kiaeromphalus* specimens described by Peel & Yochelson (1976). The stratigraphical range of this species may therefore be restricted to the middle part of the Rytteråker Formation, i.e. upper part of 7a and 7bα in Kiær's (1908) terminology (Fig. 2).

The transgressional trend from west and south across the Baltoscandian platform reached its acme during the late Aeronian of the Llandovery Epoch (Bassett et al. 1989), corresponding roughly to the distributional interval where *Kiaeromphalus* is found in Norway and Estonia. Aldridge et al. (1993) gave the name Maløykalven Secundo episode for the interval including the *sedgwickii* Graptolite Zone, representing an oceanic episode of warm-water shelf with reduced clastic input, carbonate development and abundance of corals and stromatoporoids. Both the Rumba Formation of Estonia and the Rytteråker Formation of Norway represent this shallow-water carbonate deposition, with packstones forming in a mainly low-energy environment on the seaward or offshore shelf (Bassett et al. 1989; Worsley et al. 1983; Möller 1989). Several large gastropods are found in the Rumba Formation, including *Tremanotus* cf. *T. longitudinalis* (Lindström, 1884) but they are usually preserved as internal moulds (Isakar 1990). Small platyceratids also occur, but only *Kiaeromphalus* can be readily compared with any of the gastropod species in the Rytteråker Formation. Published investigations of the gastropod fauna of this formation other than those of Kiær (1908) and Peel & Yochelson (1976) do not exist. Faunas of both formations, however, are characterized by coquinas formed by the brachiopod *Pentamerus oblongus* (Baarli & Johnson 1982; Kaljo & Einasto 1990). When comparing other fossil groups, none of the characteristic corals in the Rumba Formation (Kaljo & Einasto 1990) are recognized at species level among the fauna in the Rytteråker Formation (Neuman 1982; Aarhus 1982) while the trilobite *Calymene frontosa* Lindström, 1885 is identified in both units (Kaljo & Einasto 1990; Helbert et al. 1982). Microfossils are rare in the Rumba Formation and not particularly helpful in correlation with the Norwegian strata.

Horologium in Bohemia and Rumenia

Horologium kokeni was described by Perner (1907, pp. 293–294, pl. 106, figs. 31–32; text-fig. 224) on the basis of a single specimen from Zadní Kopanina, Bohemia, labelled as being derived from the Kopanina Formation and now preserved in the National Museum, Prague, Czech Republic. The lithology of the specimen suggests that its age is Ludlow (R. J. Horný, pers. comm. – 1998). Perner's (1907) illustrations of the holotype are comprehensive drawings which are now known to be accurate, revealing a gastropod that is morphologically very similar to *Kiaeromphalus*. The specimen was redescribed by Knight (1941, p. 152, pl. 57, fig. 2a–b) in his definitive study of the type specimens of Palaeozoic gastropod genera, but the photographs of basal and oblique lateral views failed to stimulate Peel & Yochelson (1976) to make any comparison with *Kiaeromphalus*. The single illustration of *Horologium* in Knight et al. (1960, fig. 194, 5) is inadequate.

Horný & Iordan (1994) identified a single specimen as *Horologium kokeni* from Silurian (Ludlow) strata occurring in a borehole into the East European Platform (= Moldavian Platform) succession of northern Romania. Only the upper surface of the poorly preserved specimen was illustrated.

Systematic palaeontology

Genus *Kiaeromphalus* Peel & Yochelson, 1976

Type species. – By monotypy; *Kiaeromphalus kristianiensis* Peel & Yochelson, 1976, p. 18, fig. 1A–G, from the Lower Silurian (Llandovery) Rytteråker Formation (7a–b) in the Oslo–Asker district, Oslo Region, Norway.

Kiaeromphalus undiferus (Schmidt, 1858)
Figs. 3–5

1858 *Euomphalus undiferus* n. sp., Schmidt, p. 206.
1860 *Euomphalus undiferus* Schmidt; d'Eichwald, p. 1148.
1990 *Kiaeromphalus?* sp.; Isakar, p. 64.

Lectotype. – Selected here. An internal mould (TUG 857/59) described by Schmidt (1858, p. 206) from the upper part of the Rumba Formation of Early Silurian (Llandovery, Aeronian) age, at Päri 5 km southwest of the village of Kullamaa in southwest Estonia. The specimen is 5.7 cm wide and 3.7 cm high.

Other material. – One nearly complete specimen (TUG 68/94) and partial counterpart, both showing impressions of the growth lines (width 5.7 cm and height 2.3 cm); one internal mould (TUG 41/10) of the last whorl with impressions of the growth lines (width 6 cm); one badly worn internal mould (TUG 41/9) prepared as a cross-section (width 5.5 cm and height 3.1 cm). All specimens are topotype material.

Description. – Shell large, widely phaneromphalous and low-spired, the height equal to about half the width, with 4–4.5 whorls uniformly expanding. Protoconch unknown. Whorl profile moderately convex on upper surface with rounded transition to uniformly convex and almost horizontal base, passing into a steeply inclined umbilical surface; periphery at one third of whorl height. Peripheral

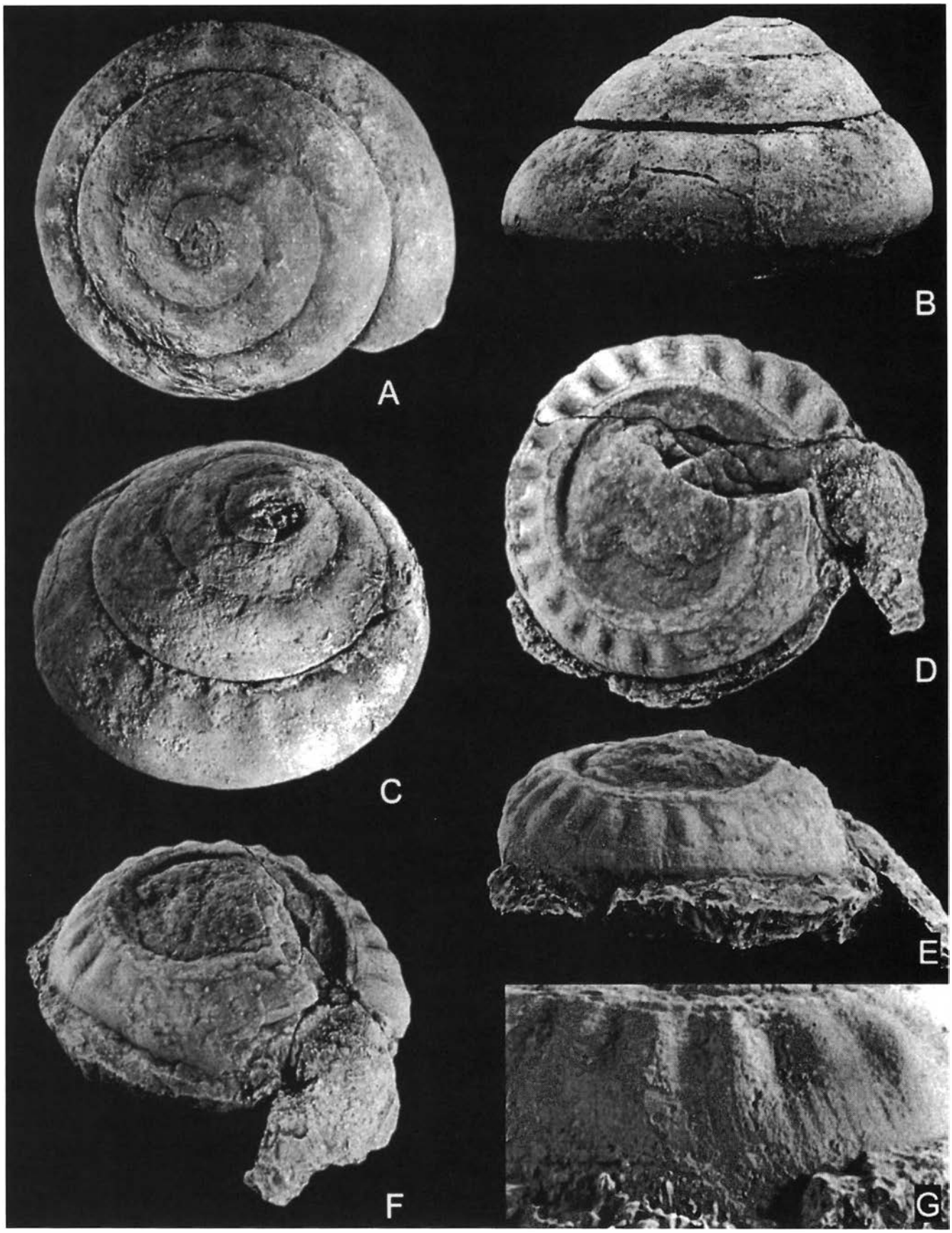

Fig. 3. Kiaeromphalus undiferus (Schmidt, 1858), upper part of the Lower Silurian (Llandovery, Aeronian) Rumba Formation at Päri 5 km SW of the Kullamaa village, SW Estonia. A–C. Dorsal, lateral and dorsal oblique views of the lectotype (TUG 857/59) described by Schmidt (1858, p. 206), × 1.5. D–G. Dorsal, lateral, dorsal oblique and detail of an internal mould (TUG 41/10) of the last whorl with impression of the growth lines, D–F ×1.5; G ×6.

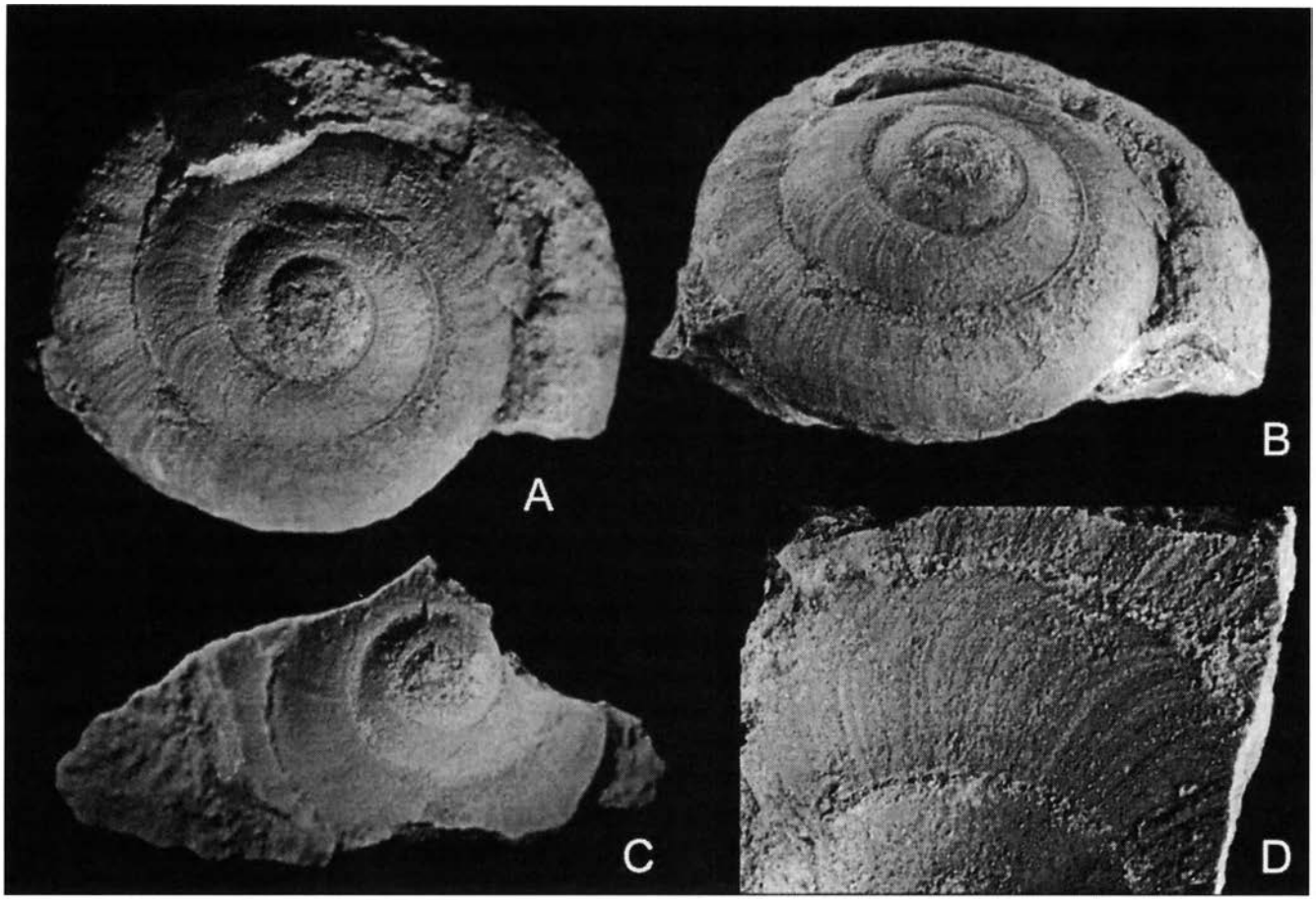

Fig. 4. Kiaeromphalus undiferus (Schmidt, 1858), upper part of the Lower Silurian (Llandovery, Aeronian) Rumba Formation at Päri 5 km SW of the Kullamaa village, SW Estonia. A–B. Dorsal and dorsal oblique views of a well-preserved specimen (TUG 68/94) with partial counter part (C–D) showing details of the growth lines. A–C ×1.5; D ×4.5.

cord developed in early ontogeny gives bevelled angularity at periphery. Umbilicus wide, nearly half of the width of the base of the whorls. Aperture radial with outer lip curving backwards (abaperturally). Ornamentation consists of numerous prosocline growth lines with increased curvature towards periphery and radially elongated and regularly spaced subsutural nodes parallel to growth lines.

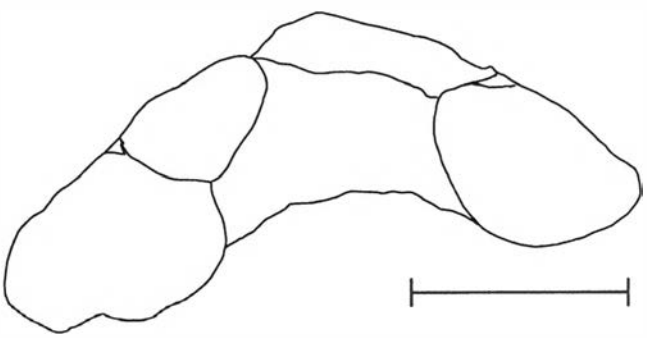

Fig. 5. Cross-section (TUG 41/9) of *Kiaeromphalus undiferus* (Schmidt, 1858), upper part of the Lower Silurian (Llandovery, Aeronian) Rumba Formation at Päri 5 km SW of the Kullamaa village, SW Estonia. Rate of whorl expansion (W), which is the width of a whorl over the width of the previous whorl, equals about 1.5. Scale bar = 1.5.

Nodes less defined in early ontogeny but the last whorl carries between 22 and 27 usually well-expressed nodes.

Remarks. – The lectotype specimen is badly worn, but the characteristic nodes developed on the upper part of the whorl surface can still be discerned. Schmidt (1858) stated that the nodes stand out only on well-preserved specimens, indicating that he had access to more than one sample. Only one specimen can be identified in Schmidt's collection (TUG, see introduction on other collections) from Päri and this is selected herein as the lectotype. Additionally, three topotype specimens of about the same size and with widely phaneromphalous shells are attributed to this species, though some morphological variation is displayed especially in the expression of the nodes and the height of the spire. The nodes seem more strongly developed in later whorls (TUG 41/10, Fig. 3D–G) when compared to the ornamentation of the Norwegian species. As with the lectotype of *K. undiferus,* the sectioned specimen (TUG 41/9, Fig. 5) is a badly worn internal mould with only faint traces of the nodes, but the shell proportions of this specimen are equal to those of the lectotype. The shell of the best-preserved specimen (TUG 68/94, Fig. 4A–D) has a much lower spire and significantly weaker nodes, though the shell is obscured by matrix on

part of the last whorl. The growth lines on this individual are similar to those of the partial specimen (TUG 41/10, Fig. 3D–G), but are only preserved on the upper whorl in both. However, considering that all the samples originate from one locality and given the overall similarities in morphology, it is concluded that the material represents one species.

The generic assignment of *Euomphalus undiferus* to *Kiaeromphalus* is based on overall similarity in shell shape and ornamentation to the type species *K. kristianiensis*. Indeed, the similarity in the shape of the growth lines and subsutural nodes may even suggest that *K. undiferus* and the type species are conspecific; the slight differences observed may reflect preservational factors. The Norwegian specimens are very distorted, but with preserved ornamentation, while the compaction of the Estonian material is generally minimal, but ornamention is lacking. The two species are of approximately the same size, widely phaneromphalous and show comparable development of subsutural nodes. Both develop a cord-like angulation in earlier whorls and show similar prosocline growth lines on the upper part of the whorl. Furthermore, they occur in contemporaneous strata of similar lithology and facies. The main difference lies in the somewhat more robust nature of the Estonian material and variation in the expression of the nodes and height of the spire within each assemblage as discussed above. Before conclusive evidence of species relationships can be put forward, better-preserved material of both species is needed for cross-sectioning and evaluation of character variation within the assemblages. In particular, the nature of the peripheral and umbilical ornamentation is currently unknown in *K. undiferus*. At the present time, separation of the two species is maintained.

K. undiferus was compared with *Stenoloron? aequilatera* (Wahlenberg, 1818) from the Wenlock of Gotland by d'Eichwald (1860). Peel & Yochelson (1976) applied a similar comparison to *K. kristianensis*. The main differences lie in the more conical shape, less deeply impressed sutures, ornamentation consisting of nodes and less strongly prosocline growth lines above the angulation in *Kiaeromphalus*. Schmidt (1858) compared *K. undiferus* with *Pleurotomaria perlata* Hall, 1852, a large discoidal gastropod from the Silurian of North America. Gubanov et al. (1995) compared *P. perlata* with their new genus *Isfarispira*, distinguished by the lack of the acute periphery seen in Hall's species, but pointed out that new and better preserved material of *P. perlata* was needed for a conclusive generic assignment.

Genus *Horologium* Perner, 1907

Type species. – By monotypy, *Horologium kokeni* Perner, 1907, pp. 293–294, pl. 106, figs. 31–32, text-fig. 224, type and only known specimen labelled Kopanina Formation at Zadní Kopanina, Bohemia. late Silurian, Ludlow.

Horologium kokeni Perner, 1907
Fig. 6

1907 *Horologium kokeni* n. sp., Perner, pp. 293–294, pl. 106, fig. 31.32, text-fig. 224.
1941 *Horologium kokeni* Perner; Knight, p. 152, pl. 57, fig. 2a–b.
1994 *Horologium kokeni* Perner; Horný & Iordan, p. 81, pl. 1, fig. 7.

Description. – Large, phaneromphalous, low-spired, trochiform gastropod with more than four whorls; apex and earliest whorls not known. Final whorl divided into an inclined, shallowly convex, slightly shouldered upper surface and a flattened, shallowly convex base by a pronounced peripheral angulation at about one-third of the whorl height; the angulation carries a flat-topped carina. Basal surface passing with increased convexity into the deep, open, umbilicus which is about one-fifth of the width of the shell in diameter. Aperture subtangential with prosocline growth lines sweeping obliquely backwards from the suture to the peripheral carina and then across the basal surface almost radially, which are slightly adapertural convexity; umbilical wall with orthocline growth lines which swing strongly adaperturally immediately prior to the suture with the previous whorl. Fine ornamentation of upper surface not preserved but growth lines followed by periodic, uniformly spaced nodes on the upper, shouldered portion of the whorl. Base with abundant, slightly wavy spiral cords crossed by fine growth lines, which become cord-like within the umbilicus. Shell thin.

Remarks. – *Horologium kokeni* has a slightly greater rate of whorl expansion than *Kiaeromphalus undiferus* (compare Figs. 3A and 4A with Fig. 6A) and a narrower umbilicus. Most significantly, the two species differ in the shape of the aperture, which is seen to be radial on the upper whorl surface in *Kiaeromphalus* and almost tangential in *Horologium*. While expression of the subsutural nodes is variable in *K. undiferus*, they are relatively wider and less numerous than in *H. kokeni*.

Homeomorphy and mode of life

Despite their apparent morphological similarity, *Kiaeromphalus* and *Horologium* have been assigned to widely separated superfamilies. Close scrutiny supports these assignments and the homeomorphy is attributed to similarities in mode of life.

Peel & Yochelson (1976) placed their new genus *Kiaeromphalus* in the family Euomphalidae by comparison with *Straparollus* (*Straparollus*) de Montfort, 1810. Wagner (1995) agreed and listed *Kiaeromphalus* in the superfamily Euomphaloidea belonging to his euomphaloid clade. This placement is well supported by the shape of the radial aperture which, following arguments developed by Linsley (1977), suggests that *K. undiferus* was sessile, living with the large shell lying flat on the sediment. Horný & Iordan (1994) suggested placement of *Horologium*

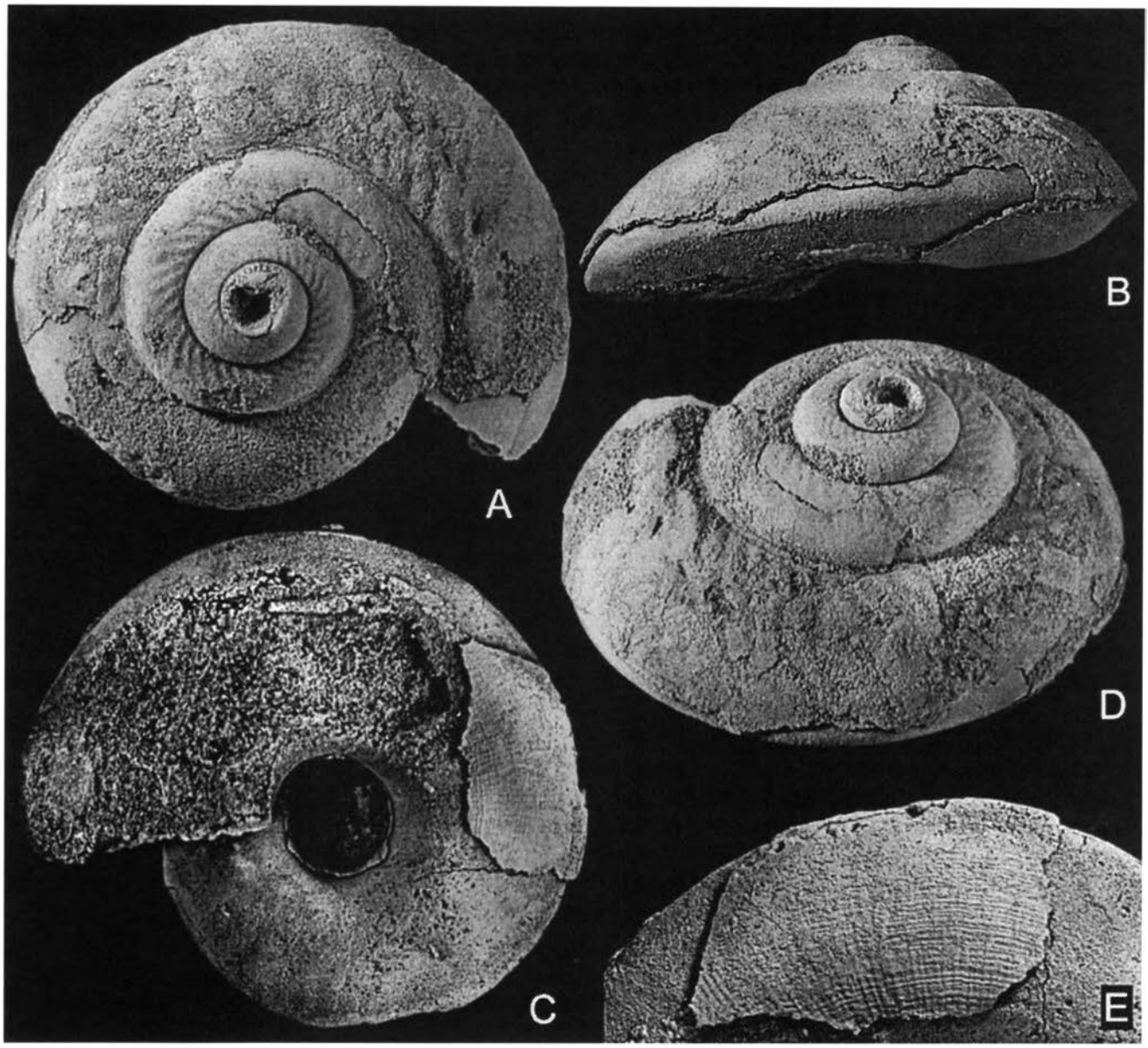

Fig. 6. Horologium kokeni Perner, 1907, from the Upper Silurian (Ludlow) part of the Kopanina Formation at Zadní Kopanina, Bohemia, Czech Republic. A–E. Dorsal, lateral, umbilical, dorsal oblique and detail views of holotype described by Perner (1907, pp. 293–294, pl. 106, figs. 31–32, text-fig. 224), A–D ×1.4, E ×2.1.

kokeni within the family Planitrochidae of the superfamily Pseudophoroidea of uncertain position (cf. Knight et al. 1960; Wagner 1995). Also here the form of the near tangential aperture supports this assignment. The strong prosocline growth lines in *Horologium* pass across the carinate periphery without deflection but the angular profile creates a location for the exhalant water current without forming a true emargination in the apertural margin. Shells with tangential apertures can clamp the aperture against the substratum when disturbed (Linsley 1977) but the narrowness of the aperture and the broad, low-spired form also suggest that *H. kokeni* spent much of its time lying flat on the substratum.

The holotype of *H. kokeni* lacks the apex, but the sedimentary infilling appears to terminate at a rounded surface (?septum) some three and a half whorls back from the aperture. The quarter of a whorl prior (adapical) to this possible septum is spar-filled with hints of other septa, and it is presumed that all the missing apical whorls were also filled with spar. The preserved spar forms a geopetal filling, indicating that the shell was inclined at about 10° to horizontal within the entombing sediment, but this may represent the hydrodynamically preferred resting-place of a transported shell rather than its life position.

An apical plug or septum that serves to close off the earliest growth stages is a quite common development within the Gastropoda and internal moulds are often seen to terminate at a regularly convex apical surface (Gubanov et al. 1995). More extensive septation is less commonly described (e.g. Yochelson 1971; Cook 1993) but in the

Silurian *Isfarispira,* Gubanov et al. (1995) noted that septa closed off up to six of the ten whorls. The withdrawal of the gastropod from the early stages was combined with rapid growth to form a multiwhorled shell as a means of increasing the surface area of the base. The low rate of whorl expansion favoured this increase by minimizing increase in the volume of the animal. Together with the formation of an umbilical flange, this high surface area growth form ('snow-shoe') was interpreted as an adaptation to life on a soft substratum (Gubanov et al. 1995). Neither *Kiaeromphalus* nor *Horologium* develop this extreme form, although the wide base and low rate of expansion of the many whorls point towards a similar adaptation.

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