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Peltura undulata n. sp. – a new olenid trilobite from the Furongian (upper Cambrian) of Scandinavia

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A new olenid trilobite species, *Peltura undulata* n. sp., is described from the Furongian (upper Cambrian) *Parabolina lobata* Zone, *Peltura* Superzone, of the Scandinavian Alum Shale Formation (Cambrian provisional Stage 10). The new species is recorded from the Oslo Region, southern Norway, Västergötland and Öland, south-central Sweden, as well as from ice-rafted boulders found in Germany. Like most other representatives of *Peltura*, the new taxon is characterised by pygidial features. It thus has a pygidium with three pairs of swellings along the posterolateral margin instead of spines, and the margin outline is undulating to some degree. In some cases the swellings are developed as broad-based semi-triangular projections. The new species, which is comparatively small, is restricted to the *Pa. lobata* Zone and accounts for up to 1/3 of the pelturid fauna, typically less. Remarks are given on the stratigraphic range of the co-occurring agnostoid *Trilobagnostus holmi*; it is inferred to be restricted to the *Pa. lobata* Zone.

**Keywords**: Cambrian, Furongian, trilobite, olenid, Alum Shale Formation, Scandinavia

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Introduction

The Alum Shale Formation of Scandinavia hosts a rich fauna of trilobites, associated with agnostoids, brachiopods, phosphatocopines, hyoliths, a.o. The Furongian shelly fauna is well described (e.g., Linnarsson, 1880; Brøgger, 1882; Westergård, 1922; Henningsmoen, 1957; Nielsen & Andersen, 2021) and comprises more than 100 trilobite species, first and foremost olenid trilobites, that are associated with less common agnostoids (see Ahlberg & Terfelt, 2012) and very rare non-olenid trilobites (Żylińska et al., 2015). Brachiopods occur at some levels. Fossils have been collected from the Alum Shale for more than 250 years and it is unusual to encounter new trilobite taxa. Here is, nonetheless, described a new species of the genus *Peltura* Milne-Edwards, 1840. Representatives of this taxon turn up at the base of the *Peltura* Superzone (regarding trilobite and agnostoid zonation of the Furongian Alum Shale, see Nielsen et al., 2014, 2020 and references therein) in the late part of the Furongian (Cambrian provisional Stage 10) and continue into the overlying latest Furongian *Acerocarina* Superzone (Fig. 1). At the moment, the genus includes eight species (Fig. 1). For synonymized names, see Henningsmoen (1957, pp. 231–232).

Rønning et al. (2020) briefly reported on a new subspecies of *Peltura scarabaeoides* from the *Parabolina lobata* Zone, treated under open nomenclature as *Pe. scarabaeoides* n. ssp. and recorded from southern Norway and south-central Sweden. Recent studies on the Furongian of Mt Kinnekulle, Västergötland, and Degerhamn, southern Öland, Sweden, recovered a fairly extensive material of this new form, which here is formally described at species level as *Peltura undulata* n. sp. It is everywhere characteristic of the *Pa. lobata* Zone along with *Peltura westergaardi*, *Trilobagnostus holmi* (Westergård, 1922), *Parabolina lobata lobata* (Brøgger, 1882) and *Parabolina lobata praecurrens* Westergård, 1944, but is much less frequent than the co-occurring *Pe. westergaardi*. 
Regarding the range of *T. holmi*, it is in most literature (e.g. Terfelt et al., 2008; Ahlberg & Terfelt, 2012; Nielsen et al., 2020, fig. 1) listed also from the older *Pe. scarabaeoides* Zone, based on a single pygidium found in the conglomerate at the top of the Alum Shale Formation at Uddagården, Falbygden, Sweden (Westergård, 1922, p. 69). This conglomerate also yielded *Peltura scarabaeoides* (Wahlenberg, 1818), *Ctenopyge pecten* (Salter, 1864) and *C. bisulcata* (Phillips, 1848), all characteristic of the *Pe. scarabaeoides* Zone. However, *T. holmi* is everywhere else in Scandinavia known exclusively from the *Pa. lobata* Zone, and the conglomerate at Uddagården, which marks an extensive hiatus, probably formed, at least in part, during the *Pa. lobata* Zone. This inference is corroborated by conodont data from the Orreholmen quarry (located some 9 km SSE of Uddagården), reported by Löfgren (1996), where reworked late Cambrian euconodont species were recorded from the lowermost Ordovician. Euconodonts did not turn up prior to the *Pa. lobata* Zone (cf. Stouge et al., 2020).

Locations of the sites referred to in this paper are shown in Fig. 2.

Systematic palaeontology

Order PTYCHOPARIIDA Swinnerton, 1915

Family OLENIDAE Burmeister, 1843

Subfamily PELTURINAE Hawle & Corda, 1847

Genus Peltura Milne-Edwards, 1840

Type species. – *Entomostracites scarabaeoides* Wahlenberg, 1818, designated by Hawle & Corda (1847).

*Peltura undulata n. sp.*

Fig. 3A–A’, Fig. 5A–F & Fig. 6K–N.
1973 *Peltura cf. scarabaeoides scarabaeoides* (Wahlenberg, 1821) – Schrank, p. 843, pl. 15, fig. 7, text-fig. 4.

2004 *Peltura cf. scarabaeoides scarabaeoides* (Wahlenberg 1821) – Mischnik, p. 117, pl. 5, fig. 2.

2005 *Peltura cf. paradoxa* (Moberg and Möller, 1898) – Ahlberg et al., p. 434, fig. 3G.

? 2014 *Peltura paradoxa*? – Bagnoli & Stouge, fig. 2.

2020 *Peltura scarabaeoides* n. ssp. – Rønning et al., p. 18, fig. 11L.

Derivation of name. – From Latin ’undulatis’ meaning wavy, alluding to the scalloped posterolateral pygidial margin of the new species.

Holotype. – Pygidium MGUH 34080 (sample DB.84) from the *Parabolina lobata* Zone (bed F) at Dagbrottet, Kinnekulle, Sweden. The holotype, which is 2.1 mm long, is illustrated in Fig. 3K, L.

Paratypes. – All other pygidia of *Pe. undulata* n.sp. illustrated in this paper are designated as paratypes.

Differential diagnosis. – Small species. Pygidium strongly resembling that of *Pe. scarabaeoides* in overall proportions (incl. axial morphology) and distribution of exterior terrace lines. The salient diagnostic feature of *Pe. undulata* n. sp. is the absence of marginal spines. Instead, three pairs of swellings, corresponding to marginal spine bases, create a gently undulating posterolateral margin although the size of the swellings varies.

Material. – Slightly more than 130 pygidia from the Oslo Region, Norway, and the Swedish provinces of Västergötland and Öland (localities are specified below). The material is thus fairly extensive, but approximately half of the pygidia at hand are fragmentary. Cranidia and free cheeks
are not differentiated from the associated pelturids (Pe. westergaardi and reworked Pe. scarabaeoides); no complete specimens of Pe. undulata n. sp. have been found so far. The material from southern Norway and Öland is preserved predominantly in anthraconite (diagenetic limestone/’stinkstone’), whereas the material from Mt Kinnekulle (Västergötland) is preserved predominantly in bioclastic limestone consisting of olenid trilobite fragments.

Repository. – Natural History Museum of Denmark (prefix MGUH).

Occurrence. – Peltura undulata n. sp. is recorded from the Oslo–Asker District (1 pygidium, Dittenkvartalet, Oslo), the Skien–Langesund District (2 pygidia, Herøya tunnel, Porsgrunn) and the Eiker–Sandsvær District (22 pygidia, Sandbakken, Vestfossen) in southern Norway (see also Rønning et al., 2020). In Sweden, the new species has been recorded in the abandoned Alum Shale quarries at Råbäck (1 pygidium), Trolmen (54 pygidia of which 3 are tentatively assigned) and Dagbrottet (31 pygidia of which 1 is tentatively assigned) on Mt Kinnekulle in Västergötland. Additional specimens have been identified in the material collected in the ‘road section’ at Degerhamn, Öland, by Rasmussen et al. (2017) (21 pygidia of which 6 are tentatively assigned). Locations of these sites are shown in Fig. 2. Logs of the Parabolina lobata Zone in Dagbrottet and Trolmen with bed numbers and faunal ranges are illustrated in Fig. 4. The material described as Pe. cf. scarabaeoides scarabaeoides by Schrank (1973) and Mischnik (2004), collected from ice-rafterd boulders in Germany, also seems to represent Pe. undulata n. sp. The new species is everywhere restricted to the Parabolina lobata Zone and it co-occurs with Peltura westergaardi, Parabolina lobata lobata, Pa. lobata praecurrens and Trilobagnostus holmi. In the sections studied on Mt Kinnekulle, Västergötland, various reworked faunal elements from the Peltura acutidens—Ctenopyge tumida and P. scarabaeoides zones are also found in the Pa. lobata Zone, including Pe.
scarabaeoides (Fig. 4A, B). The latter species has been found also in the Pa. lobata Zone at Degerhamn, Öland (unpublished data).

Description. – We have made no effort to differentiate cranidia and free cheeks of Pe. undulata n. sp., Pe. scarabaeoides and Pe. westergaardi as these skeletal parts appear nearly identical. Hence, pygidia are required for safe identification of the new species. Peltura undulata n. sp. is a comparatively small form and measured pygidia are 0.45–3.7 mm long (incl. anterior half ring). The far majority of the specimens at hand have a non-spinose, smooth margin with only minute swellings (Fig. 5A, n = 62). They are semicircular in outline (dorsal view), length:width ratio averages 0.50 (0.44–0.56, n = 51). There is a slight tendency that the smallest specimens are relatively shorter (Fig. 5B). An example of a comparatively short pygidium is illustrated in Fig. 3P.

The axis is trapezoidal in outline, fairly inflated and delimited by well-defined axial furrows. It occupies anteriorly slightly more than 0.4 (tr.) of the total width of the pygidium (w / w ratio 0.40–0.47, averaging 0.43, n = 51, Fig. 5C) and extends on average for 0.86 of the pygidial length (0.80–0.91, n = 53, Fig. 5D).

The axis consists of an anterior half ring, two axial rings and an end lobe, of which the second axial ring and the end lobe are nearly fused (e.g., Fig. 3K). The axis is approximately as wide anteriorly (tr.) as it is long (sag.) (w / l ratio 0.85–1.17, averaging 0.99, n = 52, Fig. 5E), and tapers evenly; the end lobe is ¾ as wide (tr.) as the articulating half ring (w / w ratio 0.68–0.85, averaging 0.76, n =
53, Fig. 5F). The end lobe is truncately rounded posteriorly. The axial interring furrows, of which the rear one between the second axial segment and the end lobe is nearly effaced, continue laterally into interpleural furrows that cross the pleural fields obliquely backwards to fade out close to the posterolateral margin. The anterior two furrows are well defined, whereas the short rear furrow is only vaguely discernible (e.g. Fig. 3Q). All pygidial furrows are better defined on internal moulds than in testaceous specimens, as demonstrated by the partially exfoliated axis in Fig. 3P. The forwards-slanting articulating facet stretches adaxially for c. 2/3 of the distance between the anterior corner of the pygidium and the axial furrow; there is a forward-projecting swelling at the anterior pygidial margin, where the facet stops. No border, but a convex outwards-downwards sloping 'border area' is outlined along the posterolateral margin by a dense ornament of terrace lines and the lack of cross-cutting pleural furrows (e.g., Fig. 3I, K). No marginal spines, but the posterolateral margin is variably scalloped due to three pairs of swellings in place of marginal spines. The distance between the adaxial pair of swellings corresponds approximately to the width of the anterior half ring (tr.) (e.g., Fig. 3Q). The sizes of the swellings are variable, giving rise to variation in the degree of undulation of the margin, and some specimens including the holotype have an almost smooth margin with only minute swellings (e.g. Fig. 3K, L). On other pygidia the swellings are more pronounced and extended into semi-triangular projections (e.g., Fig. 3G, X). The swellings and adjacent 'border area' are covered by distinct, long terrace lines running parallel to the pygidial margin; in well-preserved specimens, shorter terrace lines are usually visible also on the axis, following the general axial contour, as well as on the pleural fields, where they fade out adaxially (e.g., Fig. 3Q). Internal moulds show only weak or no imprints of terrace lines (e.g., Figs. 3A–C & 6L).
Comparison. – The pygidium of *Peltura undulata* n. sp. differs from those of *Pe. westergaardi* and
*Pe. scarabaeoides* by having a gently undulating posterolateral margin with three pairs of swellings
instead of marginal spines (Fig. 6).

[FIG. 6 APPROX HERE]

In comparison, *Pe. scarabaeoides* has three (rarely four) pairs of short marginal spines that typically
are bent downwards to some degree, i.e. ventrally, while *Pe. westergaardi* has three pairs of longer
and straighter marginal spines that point semi-horizontally backwards (albeit with some variation).
The pygidia of all three species have the same number of axial rings, but differ in the axial
proportions. In *Pe. undulata* n. sp. and *Pe. scarabaeoides*, the axis occupies anteriorly a little more
than 0.4 of the total pygidial width (tr.), whereas *Pe. westergaardi* has a proportionately narrower
axis occupying less than 0.4 of the total pygidial width. In *Pe. undulata* n. sp. and *Pe.
scarabaeoides*, the second axial ring and the end lobe are nearly fused; in *Pe. westergaardi*, the end
lobe is better defined by a shallow furrow (e.g., Fig. 6A). In *Pe. westergaardi*, pleural furrows are
normally visible (e.g., Fig. 6A), unlike in the two other species discussed (e.g., Figs. 3I & 6O, but
see Fig. 3M). The exterior ornamentation of terrace lines in *Pe. undulata* n. sp. is more extensive
than in *Pe. westergaardi* and strongly resembles the pattern seen in *Pe. scarabaeoides* (compare
with Fig. 6O). As pygidia of *Pe. undulata* n. sp. and *Pe. scarabaeoides* overall are similar in general
outline and ornamentation, preparation is often important for observing the marginal spines in the
latter.

The older *Peltura acutidens* has a relatively wider pygidium with three pairs of broad-based
sturdy marginal spines (e.g. Henningsmoen, 1957, pl. 25, fig. 9), and this species is readily
separated from *Pe. undulata* n. sp. Pygidia of *Peltura transiens* have short marginal spines and a
narrow border (e.g., Weidner & Nielsen, 2013, fig. 9L). Pygidia of *Peltura minor* (e.g. Nielsen & Andersen, 2021, fig. 37I), *Pe. paradoxa* (Fig. 6I, J) and *Pe. costata* (e.g. Weidner & Nielsen, 2013, fig. 9S, T) have no marginal spines, but lack marginal swellings and have a well-defined narrow border. The pelturid free cheeks found in the *Pa. lobata* Zone, assumed to include specimens from *Pe. undulata* n. sp. (as well as *Pe. westergaardi* and, on Kinnekulle and at Degerhamn, reworked *Pe. scarabaeoides*), lack a genal spine, and thus differ from the free cheeks of *Pe. transiens* and *Pe. paradoxa*, both having short genal spines.

Remarks. – A few pygidia described as *Pe. cf. scarabaeoides scarabaeoides* were reported by Schrank (1973) from glacial erratics in Germany. They were described as closely resembling *Pe. scarabaeoides*, but with rudimentary marginal spines where only the bases are present. This condition was compared to the short spines in *Pe. transiens*, but Schrank (1973) noted that the *Pe. cf. scarabaeoides scarabaeoides* pygidia lack the border characteristic of *Pe. transiens*. In the illustrated material, the distance between the inner pair of rudimentary spines is wider than the end lobe, and the end lobe is nearly fused with the second axial ring; both traits are shared with *Pe. undulata* n. sp. and the discussed specimens are here assigned to the new species. *Peltura cf. scarabaeoides scarabaeoides* was found associated with *Pe. westergaardi* and *Parabolina lobata praecurrens*, suggesting a derivation from the *Pa. lobata* Zone. Mischnik (2004) also reported pygidia of *Pe. cf. scarabaeoides scarabaeoides sensu Schrank (1973)* from glacial erratics of the *Pa. lobata* Zone found in northern Germany. Although the image quality is rather poor (Mischnik, 2004, pl. 5, fig. 2), the illustrated specimen is in all probability conspecific with *Peltura undulata* n. sp. The ice-rafted material most probably derives from the Öland–Baltic Sea area and for this reason we decided to reinvestigate the upper Furongian at Degerhamn, Öland, based on the samples originally collected by Rasmussen et al. (2017). Several pygidia of *Pe. undulata* n. sp. were found
and we consider it likely that *Peltura paradoxa?*, listed from the *Pa. lobata* Zone at Degerhamn by Bagnoli & Stouge (2014, fig. 2), represents *Pe. undulata* n. sp.

The phosphatised juvenile pygidium described from the upper *Pa. lobata* Zone at Råbäck, Västergötland, identified as *Peltura cf. paradoxa* by Ahlberg et al. (2005), is here assigned to *Pe. undulata* n. sp. It lacks the border typical of *Pe. paradoxa* (compare Fig. 6J vs. Ahlberg et al., 2005, fig. 3G).

In their preliminary description of *Pe. scarabaeoides* n. ssp., Rønning et al. (2020) emphasised distinct co-marginal terrace lines on the pygidia and a slightly narrower axial end lobe compared to *Pe. westergaardi*. The current study confirms that exterior terrace lines are more widely distributed on pygidia of *Pe. undulata* n. sp. in comparison with *Pe. westergaardi*, where comparatively sparse terrace lines are seen only along the posterolateral margin (Fig. 6A), but the description of a narrow axial end lobe seems to be based on slightly distorted material (cf. Rønning et al., 2020, fig. 11L). In pygidia of *Pe. undulata* n. sp. and *Pe. scarabaeoides*, the axis is comparatively wider than in pygidia of *Pe. westergaardi* and typically does not taper as strongly (see Fig. 6).

In the *Pa. lobata* Zone at Degerhamn, the pygidia of *Pe. undulata* n. sp. constitute 7% of the non-reworked pelturid pygidia. The corresponding figures are 12% in Dagbrottet and 6% at Trolmen, and in the upper two beds of the *Pa. lobata* Zone in Dagbrottet, the new species actually accounts for c. 1 / 3 of the non-reworked pelturid fauna. The average figure for Trolmen covers a common presence in bed B (see Fig. 4B), where *Pe. undulata* n. sp. comprises 16% of the identifiable non-reworked (?) pelturid pygidia, whereas it accounts for only 2% of the pelturid pygidia in the lower main part of the *Pa. lobata* Zone at that locality. Rønning et al. (2020) mentioned that the new (sub)species is very common in the *Pa. lobata* Zone at Vestfossen; this refers to a single limestone nodule from an unknown level within the zone.
The non-reworked pelturid material in the *Pa. lobata* Zone on Mt Kinnekulle and at Degerhamn is dominated by *Pe. westergaardi*. The pronounced difference in abundance of *Pe. undulata* n. sp. and *Pe. westergaardi* and the longer downwards range of the latter (Fig. 1) implies that these taxa cannot be interpreted just as sexual dimorphs. The function of pygidial spines is unknown, but during the range of *Peltura* it is a recurrent phenomenon that the marginal spines on the pygidium are reduced and/or disappear. It is tempting to envisage *Pe. undulata* n. sp. as a descendant of *Pe. scarabaeoides* with rudimentary pygidial spines. The co-occurring *Pe. westergaardi* has, on the contrary, proportionally much longer pygidial spines (e.g. Fig. 6A–D.).

**Conclusions**

A new olenid trilobite, *Peltura undulata* n. sp., is described from the Furongian Alum Shale Formation of Scandinavia. It is recorded from various localities in the Oslo Region, Norway, and from Mt Kinnekulle and southern Öland in south-central Sweden. It has also been found in ice-rafted boulders in Germany (with a probable derivation from the Baltic Sea area). As is typical for species of *Peltura*, the new species is characterised by pygidial characters, viz. wide axis, lack of marginal spines, variably undulating posterolateral margin, absence of a border, and extensive distribution of exterior terrace lines. The new species is smaller and less common than the associated *Peltura westergaardi*. Along with *Trilobagnostus holmi*, *Parabolina lobata lobata* and *Parabolina lobata praecurrens*, it is characteristic of the *Pa. lobata* Zone. Previous reports of *T. holmi* from the *Pe. scarabaeoides* Zone are rejected and ascribed to mixing with reworked older taxa in a conglomerate bed.
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Figure 1. Stratigraphical distribution of Peltura species. Based on Westergård (1922); Henningsmoen (1957); Terfelt (2003); Weidner & Nielsen (2013); Nielsen et al. (2020), and current study. Zonation adopted from Nielsen et al. (2020). Peltura scarabaeoides and Pe. westergaardi co-occur in the uppermost part of the Pe. scarabaeoides Zone (unpublished data from the Oslo Region and Kinnekulle, Västergötland), hence, they are separated as species rather than subspecies (see also Nielsen et al., 2020; Nielsen & Andersen, 2021). The same unpublished data indicate that last occurrence of Pe. scarabaeoides is slightly below the top of the eponymous zone. In most areas there are no or only very short overlaps between Pe. acutidens and Pe. minor (e.g. Westergård, 1922); only Terfelt (2003) reported an extensive overlap.

Figure 2. Map of southern Scandinavia showing locations of sites referred to in this paper. Approximate GPS-coordinates of the localities are listed in the right-hand column.

Figure 3. Pygidia of Peltura undulata n. sp., all from the Parabolina lobata Zone. White scale bar (in F) is 2 mm; all specimens are shown with this magnification. (A) Internal mould, Sandsbakken, sample 10221. (MGUH 34071). (B) Internal mould, Sandsbakken, sample 10221. Note semi-triangular marginal swellings. (MGUH 34072). (C) Internal mould, Sandsbakken, sample 10221. (MGUH 34073). (D) Fragmentary testaceous specimen showing external terrace line pattern. Dittenkvarтаlet, Oslo, sample 10221-II. (MGUH 34074). (E) Slightly deformed internal mould, Sandsbakken, sample 10221. (MGUH 34075). (F) Fragmentary large specimen, partially exfoliated, 3.5 mm long. Dagbrottet bed F, sample DB.62. (MGUH 34076). (G) Partially exfoliated specimen showing external terrace lines and comparatively large marginal swellings. Trolmen bed C, sample
bed E, sample TST.230. (MGUH 34091). (A’) Tiny specimen, 0.45 mm long. Trolmen bed G, sample TST.285. (MGUH 34092).

Figure 4. (A) Log of the upper 4 m of the Alum Shale section exposed in the Dagbrottet quarry, Mt Kinnekulle, Västergötland, showing the distribution of stratigraphically important taxa (various rare species as well as most reworked species have been omitted). The upper part of the section was described by Weidner & Nielsen (2013), but the shown range chart is based on extensive new fossil collections (unpublished data). (B) Log of the upper 2.9 m of the Alum Shale section exposed in the Trolmen quarry, Mt Kinnekulle, Västergötland, showing the distribution of stratigraphically important taxa. Note that only the Parabolina lobata Zone has been investigated in detail so far (unpublished). The sparse material of Parabolina heres subsp. found in bed B derives from dark-coloured reworked clasts within the bed, and, hence, must be reworked, but no subspecies of Parabolina heres are currently known from the Pa. lobata Zone anywhere else in Scandinavia. It is currently uncertain whether this bed represents the Acerocarina Superzone, in which case the remaining faunal content must be inferred reworked.

Figure 5. (A) Diagram showing size distribution of the measurable pygidia at hand (sagittal length). (B–F) Scatter plots of various pygidial features of Peltura undulata n. sp. plotted against length of pygidium. Especially the width of axis (both anterior and posterior) is difficult to measure precisely, probably adding to data scatter. All measurements were made on photographs using Adobe Photoshop.
Figure 6. Comparison of pygidia of Peltura undulata n. sp. with representatives of Peltura closest in age. The specimens are from the Parabolina lobata Zone unless otherwise stated (Trolmen bed B is tentatively assigned to this zone, see Fig. 4B). Regarding localities on Bornholm, see Nielsen & Andersen (2021). White scale bar is 2 mm; all specimens are shown with this magnification. Peltura westergaardi (A–H). (A) Well-preserved large testaceous pygidium showing exterior terrace line pattern. Dagbrottet bed F, sample DB.45. (MGUH 34093). (B) Partially exfoliated pygidium with well-preserved long marginal spines. Note that the outer pair bends slightly upwards and that the second pair bends slightly downwards, which is unusual. Trolmen bed C, sample TST.128. (MGUH 34094). (C) Partially exfoliated pygidium showing exterior terrace line pattern and well-defined furrows. Dagbrottet bed F, sample DB.36. (MGUH 34095). (D) Smaller pygidium with comparatively sturdy marginal spines. Trolmen bed B, sample TST.45A. (MGUH 34096). (E) Internal mould of smaller pygidium with comparatively sturdy marginal spines. Trolmen bed H, sample TST.329. (MGUH 34097). (F) Internal mould of small pygidium. Note the comparatively short marginal spines. Dagbrottet bed I, uppermost Peltura scarabaeoides Zone, sample DB.201. (MGUH 34098). (G) Internal mould of small pygidium. Note the comparatively short marginal spines. Dagbrottet bed J, uppermost Peltura scarabaeoides Zone, sample DB.234. (MGUH 34099). (H) Fragmentary transitory pygidium. Dagbrottet bed G, sample DB.128G. (MGUH 34100). Peltura paradoxa (I, J). (I) Partially exfoliated pygidium. Note border outline and smooth posterolateral margin. Parabolina heres megalops Zone, Slemmestad, lower nodule level (see Nielsen et al., 2020, fig. 8), sample 102161B. (MGUH 34101). (J) Internal mould showing weakly discernible imprints of exterior terrace lines. Parabolina heres megalops Zone, Slemmestad, lower nodule level (see Nielsen et al., 2020, fig. 8), sample 102161A.
(MGUH 34102). **Peltura undulata** n. sp. (K–N). (K) Partially exfoliated large pygidium, 2.9 mm long. Trolmen bed B, sample TST.89. (MGUH 34103). (L) Internal mould of medium- sized pygidium with comparatively large marginal swellings. Trolmen bed B, sample TST.61B. (MGUH 34104). (M) Internal mould of smaller pygidium. Imprints show distribution of exterior terrace lines. Degerhamn bed 21 (see Rasmussen et al., 2017), sample DE.20. (MGUH 34105). (N) Well-preserved small pygidium showing distribution of exterior terrace lines. Dagbrottet bed F, sample DB.ATN.532. (MGUH 34106). **Peltura scarabaeoides** (O–U). (O) Fairly well-preserved large pygidium showing distribution of exterior terrace lines and comparatively long, ventrally directed marginal spines. Læså, loc. 6 (Bornholm), Peltura scarabaeoides Zone, sample GM 1871–626. This specimen has previously been illustrated by Nielsen & Andersen (2021, fig. 38E). (MGUH 33908). (P) Internal mould of relatively short and wide pygidium. Ekedalen, Peltura scarabaeoides Zone, sample EK-21_3. Compare with specimen illustrated in T. (MGUH 34107). (Q) Small pygidium with downwards- directed spines. Læså between Hjulmagergård and Vasagård, (Bornholm), Peltura scarabaeoides Zone, sample GM 1871.626 (MGUH 34108). (R) Small pygidium with downwards- directed spines. Læså, loc. 6 (Bornholm), Peltura scarabaeoides Zone, sample GM 1922.142S (MGUH 34109). (S) Medium- sized pygidium showing distribution of exterior terrace lines. Loose boulder, ’cementen’, Øleå (Bornholm), Peltura scarabaeoides Zone, sample GM 1874.27 (MGUH 34110). (T) Internal mould of medium-sized pygidium with strongly downwards- directed marginal spines (not visible in dorsal view). Note also imprints of widely distributed exterior terrace lines. Dagbrottet bed A (reworked), sample DB.ATN.193. (MGUH 34111). (U) Comparatively small pygidium with downwards- directed marginal spines. Læså,
probably loc. 6 (Bornholm), Peltura scarabaeoides Zone, sample GM 1877.1999 (MGUH 34112).

Figure 1. Stratigraphical distribution of Peltura species. Based on Westergård (1922); Henningsmoen (1957); Terfelt (2003); Weidner & Nielsen (2013); Nielsen et al. (2020), and current study. Zonation adopted from Nielsen et al. (2020). Peltura scarabaeoides and Pe. westergaardi co-occur in the uppermost part of the Pe. scarabaeoides Zone (unpublished data from the Oslo Region and Kinnekulle, Västergötland), hence, they are separated as species rather than subspecies (see also Nielsen et al., 2020; Nielsen & Andersen, 2021). The same unpublished data indicate that last occurrence of Pe. scarabaeoides is slightly below the top of the eponymous zone. In most areas there are no or only very short overlaps between Pe. acutidens and Pe. minor (e.g. Westergård, 1922); only Terfelt (2003) reported an extensive overlap.
Figure 2. Map of southern Scandinavia showing locations of sites referred to in this paper.

Approximate GPS-coordinates of the localities are listed in the right-hand column.
Figure 3. Pygidia of Peltura undulata n. sp., all from the Parabolina lobata Zone. White scale bar (in F) is 2 mm; all specimens are shown with this magnification. (A) Internal mould, Sandsbakken, sample 10221. (MGUH 34071). (B) Internal mould, Sandsbakken, sample 10221. Note semi-triangular marginal swellings. (MGUH 34072). (C) Internal mould, Sandsbakken, sample 10221. (MGUH 34073). (D) Fragmentary testaceous specimen showing external terrace line pattern. Dittenkvartalet, Oslo, sample 10221-II. (MGUH 34074). (E) Slightly deformed internal mould, Sandsbakken, sample 10221. (MGUH 34075). (F) Fragmentary large specimen, partially exfoliated, 3.5 mm long. Dagbrottet bed F, sample DB.62. (MGUH 34076). (G) Partially exfoliated specimen showing external terrace lines and comparatively large marginal swellings. Trolmen bed C, sample TST.114A. (MGUH 34077). (H) Partially exfoliated specimen. Degerhamn, bed 20.2 (see Rasmussen et al., 2017), sample DE.42. (MGUH 34078). (I, J) Well-preserved testaceous specimen showing external terrace lines, and a nearly smooth margin with only small swellings, dorsal and rear view. Dagbrottet bed F, sample DB.83. (MGUH 34079). (K, L) Holotype. Well-preserved testaceous specimen showing external terrace lines, and a nearly smooth margin with only minute swellings, dorsal and oblique rear view. Dagbrottet bed F, sample DB.84. (MGUH 34080). (M, N) Slightly distorted specimen with well-preserved test showing external terrace lines, dorsal and oblique rear view. Dagbrottet bed F, sample DB.66. (MGUH 34081). (O) Fairly well-preserved testaceous specimen showing external terrace line pattern. Dagbrottet bed F, sample DB.27. (MGUH 34082). (P) Comparatively short and wide pygidium, 1.5 mm long. Compare with short Peltura scarabaeoides pygidium, Fig. 6P. Dagbrottet bed H, sample DB.167. (MGUH 34083). (Q, R) Well-preserved testaceous specimen showing external terrace lines and small marginal swellings, dorsal and oblique rear view. Dagbrottet bed F, sample
DB.ATN.529. (MGUH 34084). (S, T) Fairly well-preserved smaller testaceous specimen showing external terrace lines and small marginal swellings, dorsal and oblique rear view.

Dagbrottet bed F, sample DB.21. (MGUH 34085). (U) Fragmentary specimen showing well-preserved external terrace lines.

Trolmen bed B, sample TST.89. (MGUH 34086). (V) Small specimen with comparatively distinct triangular marginal swellings.

Trolmen bed G, sample TST.262. (MGUH 34087). (W) Fragmentary smaller specimen, 1.4 mm long, but much narrower than the specimen illustrated in P. Dagbrottet bed H, sample DB.156. (MGUH 34088). (X) Smaller, partially exfoliated specimen showing comparatively distinctive furrows.

Trolmen bed E, sample TST.217A. (MGUH 34089). (Y) Smaller specimen.

Trolmen bed B, sample TST.83. (MGUH 34090). (Z) Small specimen.

Trolmen bed E, sample TST.230. (MGUH 34091). (A') Tiny specimen, 0.45 mm long.

Figure 4. (A) Log of the upper 4 m of the Alum Shale section exposed in the Dagbrottet quarry, Mt Kinnekulle, Västergötland, showing the distribution of stratigraphically important taxa (various rare species as well as most reworked species have been omitted). The upper part
of the section was described by Weidner & Nielsen (2013), but the shown range chart is
based on extensive new fossil collections (unpublished data). (B) Log of the upper 2.9 m of
the Alum Shale section exposed in the Trolmen quarry, Mt Kinnekulle, Västergötland,
showing the distribution of stratigraphically important taxa. Note that only the
Parabolina lobata Zone has been investigated in detail so far (unpublished). The sparse
material of Parabolina heres subsp. found in bed B derives from dark-coloured reworked
clasts within the bed, and, hence, must be reworked, but no subspecies of Parabolina
heres are currently known from the Pa. lobata Zone anywhere else in Scandinavia. It is
currently uncertain whether this bed represents the Acerocarina Superzone, in which case
the remaining faunal content must be inferred reworked.
Figure 5. (A) Diagram showing size distribution of the measurable pygidia at hand (sagittal length). (B–F) Scatter plots of various pygidial features of Peltura undulata n. sp. plotted against length of pygidium. Especially the width of axis (both anterior and posterior) is difficult to measure precisely, probably adding to data scatter. All measurements were made on photographs using Adobe Photoshop.
Figure 6. Comparison of pygidia of Peltura undulata n. sp. with representatives of Peltura closest in age. The specimens are from the Parabolina lobata Zone unless otherwise stated (Trolmen bed B is tentatively assigned to this zone, see Fig. 4B). Regarding localities on Bornholm, see Nielsen & Andersen (2021). White scale bar is 2 mm; all specimens are shown with this magnification. Peltura westergaardi (A–H). (A) Well-preserved large testaceous pygidium showing exterior terrace line pattern. Dagbrottet bed F, sample DB.45. (MGUH 34093). (B) Partially exfoliated pygidium with well-preserved long marginal spines. Note that the outer pair bends slightly upwards and that the second pair bends slightly downwards, which is unusual. Trolmen bed C, sample TST.128. (MGUH 34094). (C) Partially exfoliated pygidium showing exterior terrace line pattern and well-defined furrows. Dagbrottet bed F, sample DB.36. (MGUH 34095). (D) Smaller pygidium with comparatively sturdy marginal spines. Trolmen bed B, sample TST.45A. (MGUH 34096). (E) Internal mould of smaller pygidium with comparatively sturdy marginal spines. Trolmen bed H, sample TST.329. (MGUH 34097). (F) Internal mould of small pygidium. Note the comparatively short marginal spines. Dagbrottet bed I, uppermost Peltura scarabaeoides Zone, sample DB.201. (MGUH 34098). (G) Internal mould of small pygidium. Note the comparatively short marginal spines. Dagbrottet bed J, uppermost Peltura scarabaeoides Zone, sample DB.234. (MGUH 34099). (H) Fragmentary transitory pygidium. Dagbrottet bed G, sample DB.128G. (MGUH 34100). Peltura paradoxa (I, J). (I) Partially exfoliated pygidium. Note border outline and smooth posterolateral margin. Parabolina heres megalops Zone, Slemmestad, lower nodule level (see Nielsen et al., 2020, fig. 8), sample 102161B. (MGUH 34101). (J) Internal mould showing weakly discernible imprints of exterior terrace lines. Parabolina heres megalops Zone, Slemmestad, lower nodule level (see Nielsen et al., 2020, fig. 8), sample 102161A.
probably loc. 6 (Bornholm), Peltura scarabaeoides Zone, sample GM 1877.1999 (MGUH 34112).