Clitambonitoid brachiopods from the Middle and Upper Ordovician of the Oslo Region, Norway

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Vinn, O. & Spjeldnæs, N. Clitambonitoid brachiopods from the Middle and Upper Ordovician of the Oslo Region, Norway. *Norsk Geologisk Tidsskrift,* Vol. 80, pp. 275–288. Oslo 2000. ISSN 0029-196X.

Nine species of clitambonitoid brachiopods have been described from the Middle and Upper Ordovician of the Oslo Region, Norway. They include, *Hemipronites*? sp., *Clitambonites schmidti, Clinambon anomalus, Ilmarinia dimorpha, Vellamo oandoensis, Kullervo hibernica, Kullervo* aff. *parva, Kullervo* aff. *punctata* and *Kullarvo* cf. *lacunata.* The palaeobiogeography and palaeoecology of the Upper Ordovician clitambonitoid brachiopods are discussed. The species found in the northern and western parts of the Oslo Region are mostly related to those of the Baltic carbonate platform, despite surprisingly large differences in lithology. The foreland basin (the Oslo-Scania confacies belt of Jaanusson & Bergstrøm, 1980) has a different fauna, dominated by pandemic species of *Kullervo.* This genus is supposed to have developed in parallel in Avalonia (pandemic species and the North American species) and Baltica (all endemic species to Baltica), from an early kullervo of either Baltic or Avalonian origin. The rapid spread of the genus in the North Atlantic area is linked – in time – to the large bentonite in the Middle Caradocian.

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Introduction

The Lower Ordovician clitambonitoids of the Oslo Region (Fig. 1) are well known and have been described, among others, by Öpik (1939); much less studied are those of the Upper Ordovician. However, one of the authors (N. Spj.) has studied them sporadically as a continuation of the "*Chasmops*" project (cf. Størmer 1953, pp. 38–41). Because of the small number of specimens and the lack of comparative material, progress was slow until establishment of the present cooperative venture.

The few references to clitambonitoids from the Upper Ordovician of the Oslo Region include: "*Clitambonites* cf. *schmidti*" of Størmer (1953, p. 64), from what is now the Arnestad Formation at Slependen in Asker and which is a specimen of *Kullervo*. Opalinski & Harland (1981) mentioned (based on information from Spjeldnæs) *Vellamo* sp. (*V. oandoensis*) from the Mjøsa Formation. Spjeldnæs (1982, p. 156) mentioned *Kullervo* from Furuberget in the Hamar–Nes District (Mjøsa), and the migrations of *Kullervo* were discussed by Spjeldnaes (1978, pp. 142, 145; and 1984, p. 223). Finally, Owen et al. (1990, p. 22) noted *Kullervo* cf. *lacunata* Öpik – determined by D. A. T. Harper – from the Arnestad Formation in the Oslo–Asker District (Fig. 2).

As is usual in the Oslo Region Ordovician, much of the material is preserved as moulds, but the photographic figures are based mostly on latex replicas, in order to facilitate comparisons with the better preserved Estonian and American material.

In the present paper, the focus is on the taxonomy and ecology of Norwegian Upper Ordovician clitambonitoids, as well as on their palaeobiogeography and stratigraphical distribution within the Baltica and beyond. The term Middle Ordovician is used here for the interval from the base of *Tripodus laevis* conodont Biozone to the top of *Nemagraptus gracilis* graptolite Biozone, or in terms of Baltic stages from Volkhovian to upper Uhakuan (Webby 1998).

Systematic descriptions

Repositories. – All the specimens used in this study belong to the Palaeontological Museum, University of Oslo (PMO).

Abbreviations appearing in the text are as follows: L = maximum length, W = maximum width. All measures are in mm.

Suborder Clitambonitidina Öpik, 1934

Superfamily Gonambonitoidea Winchell et Schuchert, 1895

Family Kullervoidae Öpik, 1934

Genus *Kullervo* Öpik, 1932

Remarks on occurrence

One of the most perplexing observations in this study is the high number of sympatric species of *Kullervo* (in Fangberget 2, in Arnestadtangen 2, in Bratterud 3, and in even Billingstad 4). According to the current species criteria for *Kullervo*, there are distinct categories in the

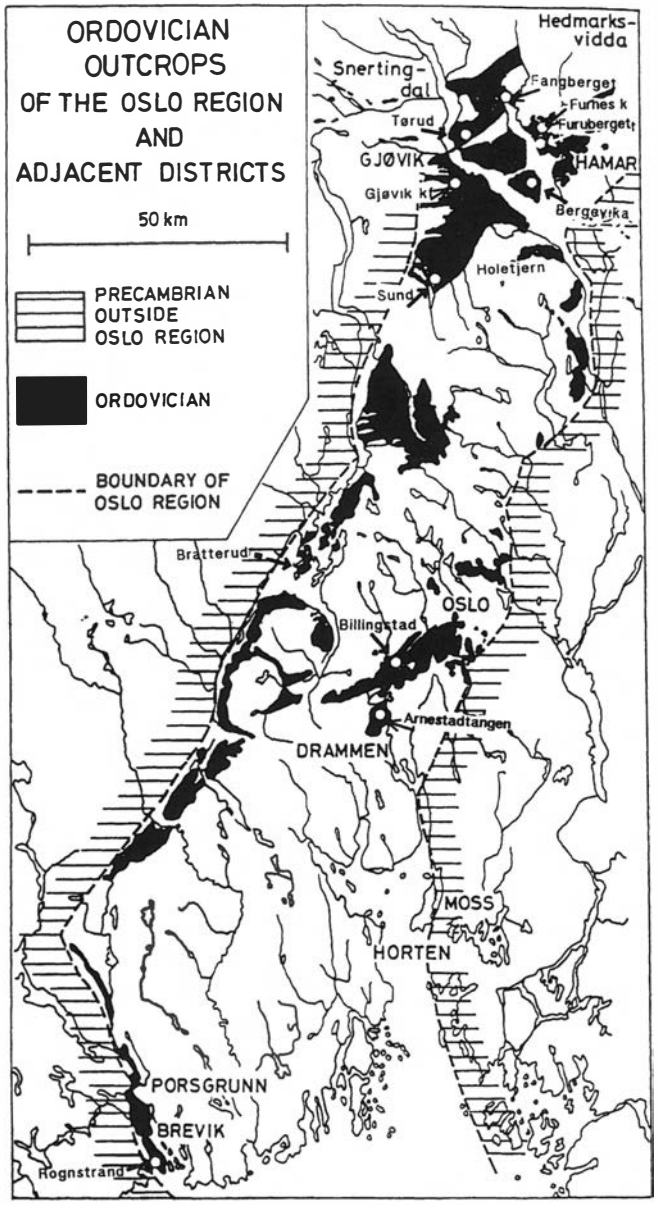


Fig. 1. Locality map of the Oslo Region showing the main localities of Middle and Upper Ordovician clitambonitoids.

material present. This can be explained in two ways: either there may have been ecological niches, not recorded in the sediments, and not seen in the rest of the genera of brachiopods, with separate *Kullervo* species, or the presently used species concept of *Kullervo* is not really valid, and the species are much more variable than previously supposed.

Further studies on the variability in larger – as yet unavailable – populations of *Kullervo* are needed to resolve this problem.

Kullervo hibernica Harper, 1952

Figs. 4, A–P, 5J–M, X; 6A–G.

1952 *Kullervo hibernica* n.sp. – Harper, pp. 100–101, pl. 6, figs. 6,7. 1980 *Kullervo* sp. – Hiller, p. 171, fig. 239. 1994 *Kullervo* aff. *hibernica* – Parkes, p. 154, pl. 9, figs. 6, 9.

Material. – One shell (PMO 162.085, L = 9.0, W = 16.0;), four dorsal valves (PMO 162.079, L = 13.0, W = 17.0; PMO 162.068, L = 11.5, W = 15.0), eight ventral valves (PMO 162.080, L = 17.0, W = 20.0; PMO 162.081, L = 14.0, W = 14.0; PMO 162.088, L = 17.0, W = 19.0; PMO 162.089, L = ????, W = 16.0; PMO 162.091, L = 14.0, W = 16.0), two moulds of the ventral exteriors, one ventral interior (PMO 162.087), five dorsal interiors (PMO 162.069; PMO 162.090, L = 14.0, W = 11.5) and probably one mould of the ventral interior.

Locality and horizon. – Ventral valves from the Arnestad Formation (Caradoc) at Bratterud in Ringerike. Dorsal interior and exterior from the Arnestad Formation at Billingstad and Arnestadtangen in Asker, from the Furuberget Formation at Fangberget Nord in Ringsaker, and from the same formation at Furuberget in the Hamar–Nes District, and from Sund, at Einavann in the southernmost part of the Toten District, in beds with *Scopelochasmops conicopthalmus*, probably corresponding in age to the upper part of the Arnestad Formation, and possibly also partly to the, Furuberget Formation (Caradoc, Upper Ordovician).

Description. – Shell subpentagonal, mature specimens 60–90% as long as wide with the maximum width at mid-length, immature specimens usually as long as wide with the maximum width at the hingeline, but also not remarkably less wide at mid-length of the shell. Anterior commissure gently sulcate, anterior margin straight or gently rounded. Cardinal extremities obtuse to acute, sides posterolaterally straight or slightly concave.

Radial ribs bifurcating, in maximum with two branchings, on average five ribs per 5 mm along the anterior margin in the adult specimens. Number of primary ribs 7–9 in ventral valve and 6–9 in dorsal valve. Lateral sectors without or with the weakly developed radial ribs clearly subordinate to the concentric ornament.

The whole shell is covered with fine, on average 0.2 mm wide, evenly spaced concentric ridges. In the dorsal valve the concentric ridges become gradually more closely spaced in the postero-anterior direction. Frequency of the ridges per 5 mm of valve length, measured medianly anterior to the 5 mm growth stage, is 7–10 in ventral valves and 14–25 in the dorsal valves.

Ventral valve strongly convex, with flat to curved surface in the lateral profile, one specimen (PMO 162.080) is unevenly convex, subcarinate, the low median fold originating about mid-length in the same slightly more than 1/3 as wide as shells width.

Ventral interarea of long, triangular to subtriangular, flat to gently concave, apsacline, about 70% as long as wide. Delthyrium about 30–45% as wide as hingeline and about 50–90% as wide as long. Deltidium long, almost flat to moderately convex, projecting 0.6–1.4 mm away from the

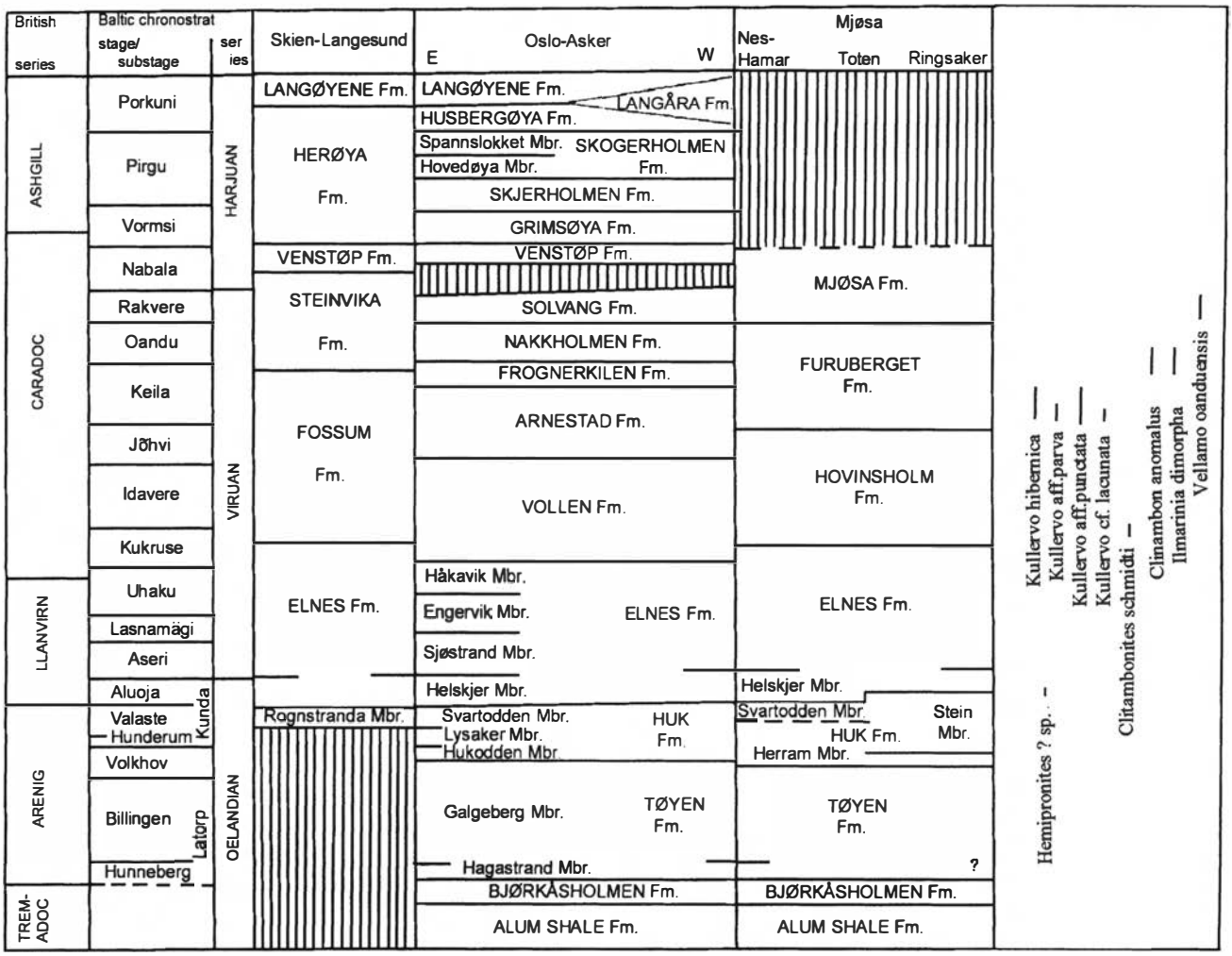


Fig. 2. Stratigraphical units (Owen et al. 1990; Webby 1998) and biostratigraphical distribution of clitambonitoids in the Middle and Upper Ordovician of the Oslo Region.

surface of the interarea. Foramen moderate to large, rounded, functional, subapical, with diameter of 1.0–2.0 mm, in smaller specimen just in the middle of deltidium, about 2.0 mm from the apex in two complete valves (PMO 162.080; 162.081) (Fig. 3C).

Dorsal valve considerably flatly convex, with the moderate to wide shallow sulcus originating in the umbonal part of valve, on average half as wide as valve, bounded by gently convex flanks with flattening over lateral extremities. Dorsal sulcus about one-third as wide as the valve width anteriorly. Dorsal interarea short relative to valve length, nearly catacline to slightly anacline, notothyrium 3/4 covered by gently convex chilidium, projecting 1.1 mm away from surface of interarea (PMO 162.068).

Ventral interior with the spondylium triplex with hemisyrinx (Fig. 3B). The lateral septa of spondylium extending valve floor in the umbonal part of the valve.

Cardinal process prominent. Socket walls divergent about two times as wide as long, merging anteromedianly with the notothyrial platform, continuing laterally from the sockets in the form of narrow, low, posteriorly incurved ridges which surround sockets latero-anteriorly, extending nearly cardinal extremities. Median ridge emerging from notothyrial platform, posteriorly slightly lower than platform, highest and widest at mid-length of valve. About at the mid-length of the valve the median ridge tapers into a thin, low median septum, reaching anteriorly two-thirds valve length. Dorsal adductor field subpetaloid, impressed on shell floor, extending to about two-thirds valve length. Anterior adductor scars tongue-shaped, slender, longer, but seem to be slightly smaller than posterior ones, with the strongly raised anteriors. The posterior adductor scars subtriangular, between anterior scars and socket walls.

Discussion. – The Norwegian specimens described can be identified with *K. hibernica* on the basis of its holotype, the dorsal valve, with nearly identical interior. The type species is described from the Knockerk House Sandstone Member of Lower Caradoc Knockerk Formation at Grangegeeth, Ireland (Harper 1952; Romano 1980).

The Norwegian material is better preserved than the type one. However, the incomplete nature of the holotype does not enable comparison of all characters, especially in

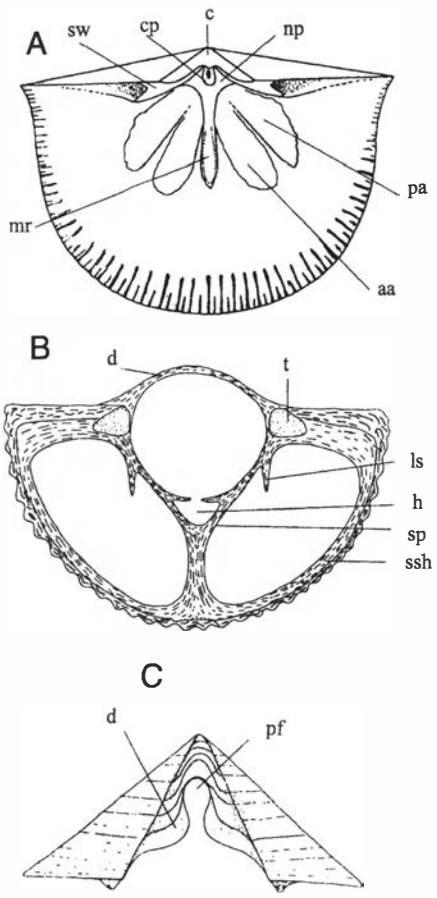


Fig. 3. A. Generalized illustration of the dorsal valve of the kullervos showing typical morphological features to the *Kullervo hibernica,* aa – anterior adductor scars, c – chilidium, cp – cardinal process, mr – middle ridge, np – notothyrial platform, pa – posterior adductor scars, sr – subperipheral rim, sw – socket ridge. B. Section through spondylium triplex of the pedicle valve of *Kullervo* aff. *punctata*, d – deltidium, h – hemisyrinx, ls – lateral septum, sp – spondylium, ssh – secondary shell, t – tooth. C. Stylized reconstraction of the pedicle foramen of immature *Kullervo hibernica*, illustrating the possible forming of subapical foramen, d – deltidium, pf – pedicle foramen.

the part of cardinalia and the ventral valve. The only difference is in the length of the thin median septum, which is longer in the holotype (NMING: F14034; Parkes 1994, p. 154, pl. 9, fig. 18), but it could also be result of the mode of preservation. The rest of the specimens described by Parks (1994, p. 154, pl. 9) as *K.* aff. *hibernica* have not been included in the synonymy list here, mostly because the characters typical for the species were not sufficiently recognizable on the photographs.

The incomplete specimen described by Hiller (1980, p. 171, fig. 239) from the upper part of the Dolhir Formation (middle Ashgill) of the Glyn Ceiriog District, north Wales, is assigned to species because of the ornamentation and outline, being typical for *K. hibernica.*

Kullervo aff. *parva*

Figs. 4Q–Y

Material. – Two ventral valves (PMO 162.074, L = 12.5, W = 11.0; PMO 162.077) and one dorsal valve (PMO 162.078, L = 11.0, W = 14.5). One mould of the dorsal interior (PMO 162.075), and a mould of the ventral interior (PMO 162.076).

Locality and horizon. – Billingstad, Asker; Arnestad Formation, just below big (Kinnekulle) bentonite, (Upper Ordovician).

Description. – Shell ventribiconvex, clearly subpentagonal in outline, on average 90% as wide as long, with the maximum width along the hingeline. Anterior margin straight, commissure sulcate. Cardinal extremities acute. Sides usually nearly straight, becoming gently concave posteriorly.

Radial ribs bifurcating, 11 ribs per 5 mm along anterior margin in the ventral valve and 13 in dorsal valve. Number of primary ribs in umbonal area 6–7. The ribs are lacking or less developed on cardinal extremities.

Concentric ridges cover whole shell, 4–15 per 5 mm of valve length, measured medianly anterior to 5 mm growth stage, in two ventral valves.

Ventral valve strongly convex in lateral profile, convex and medianly flat in transverse profile, with faint sulcus originating umbonally. Ventral interarea long triangular, moderately to strongly apsacline, concave in lateral profile, about half as wide as long. Delthyrium about 40% as wide as the hingeline and about 75% as wide as long. Deltidium convex, projecting 1.2 mm away from surface of interarea. Foramen small, functional in two specimens studied; apical when entirely open (PMO 162.077), or slightly subapical (PMO 162.074) when partially filled by secondary shell, with the diameter of 1.0 mm.

Dorsal valve strongly convex in both profiles with sulcus originating umbonally. Dorsal interarea long (about 2.5 mm), moderately anacline, flat. Chilidium gently convex, with W shaped distal edge.

Ventral interior with spondylium triplex. Subspondylial lateral septa rudimentary, reaching the valve floor in umbonal part.

Cardinal process thin, plate-like, continuous with the chilidium. Socket walls divergent, about three times as wide as long, extending slightly further than half valve width, proceeding antero-laterally from the sockets in form of a narrow posteriorly incurved ridges, reaching nearly the four-fifths valve width. Socket walls merge anteromedianly with the notothyrial platform. Median ridge weakly developed, slender, long, posteriorly half as wide as socket walls, continuous with the notothyrial platform, but clearly lower, extending to the margin of the adductor field. Notothyrial platform triangular. Dorsal adductor field subpetaloid, impressed on floor of the shell, extending to about three-fourths valve length. The anterior adductor scars gently divergent, less divergent than posterior pair. Anterior pair of the adductor scars slightly greater, steeper, clearly longer, and more strongly expressed than posterior pair, with the gently raised anteriors.

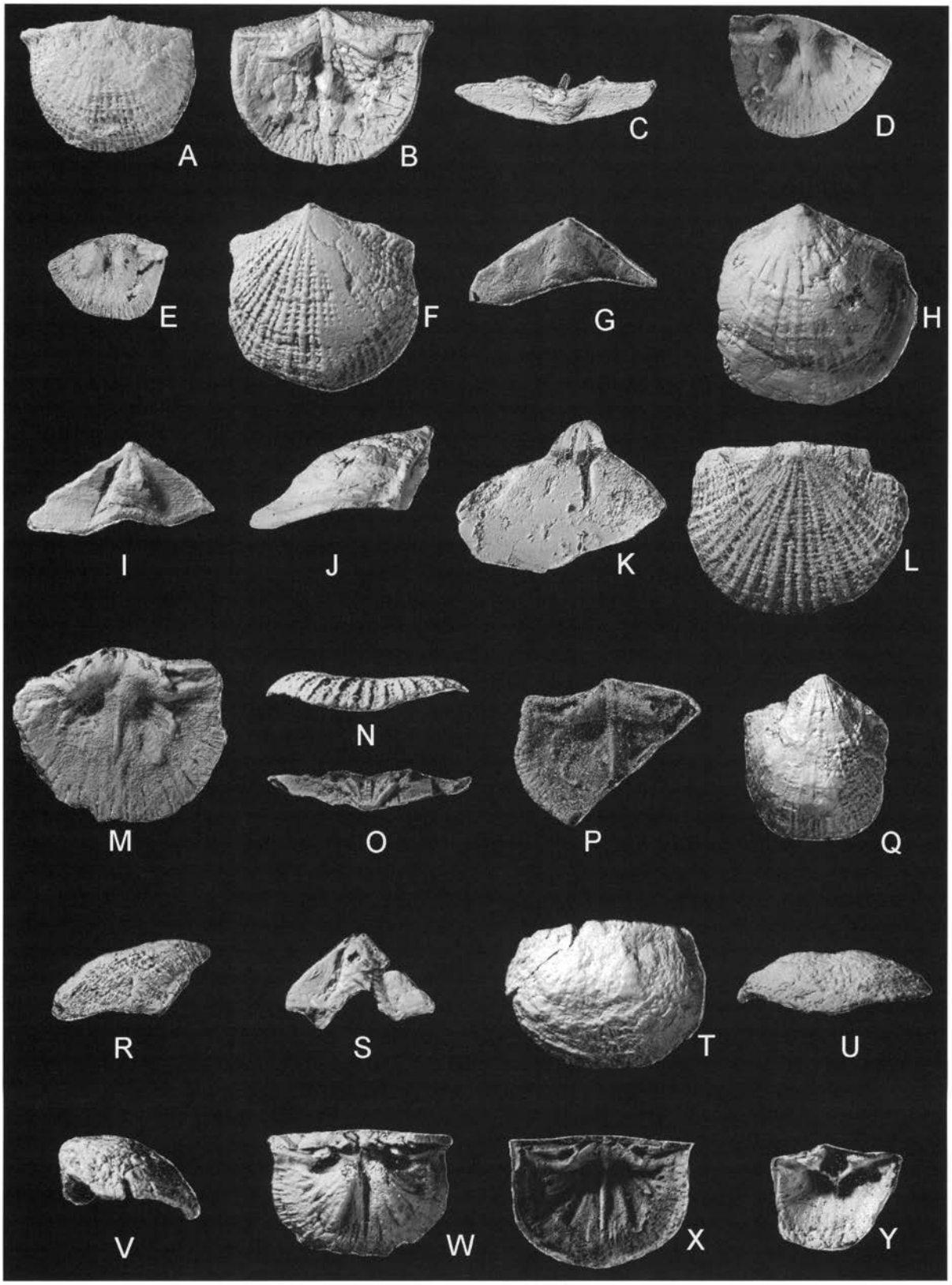


Fig. 4. A–C. *Kullervo hibernica* Harper, 1952, PMO 162.068. Dorsal valve, Billingstad, Arnestad Formation, ×2. D. *Kullervo hibernica* Harper, 1952, PMO 162.069. Dorsal interior, latex cast, ×2.0. E. *Kullervo hibernica* Harper, 1952, PMO 162.069. Impression of the dorsal interior, Billingstad, Arnestad Formation, ×1.5. F–G. *Kullervo hibernica* Harper, 1952, PMO 162.081, ventral valve, Arnestadtangen, Arnestad Formation, ×2.4. H–J. *Kullervo hibernica* Harper, 1952, PMO 162.080, ventral valve, Bratterud, Arnestad Formation, ×2. K. *Kullervo hibernica* Harper, 1952, PMO 162.087, impression of the ventral interior, Bratterud, Arnestad Formation, ×2. L–O. *Kullervo hibernica* Harper, 1952, PMO 162.079, dorsal valve, Bratterud, Arnestad Formation, ×2.2. P. *Kullervo hibernica* Harper, 1952, PMO 162.080, latex cast from the impression of the dorsal interior, Arnestadtangen, Arnestad Formation, ×2.2. Q–S. *Kullervo* aff. *parva*, PMO 162.074, ventral valve, Billingstad, Arnestad Formation, ×2.4. T–V. *Kullervo* aff. *parva*, PMO 162. 077, dorsal valve, Billingstad, Arnestad Formation, ×2.4. W. *Kullervo* aff. *parva*, PMO 162.075, impression of the dorsal interior, Billingstad, Arnestad Formation, ×2.4. X. *Kullervo* aff. *parva*, PMO 162.075, latex cast, ×2.4. Y. *Kullervo* aff. *parva*, PMO 162.076, latex cast from the impression of the ventral interior, Billingstad, Arnestad Formation, ×2.4.

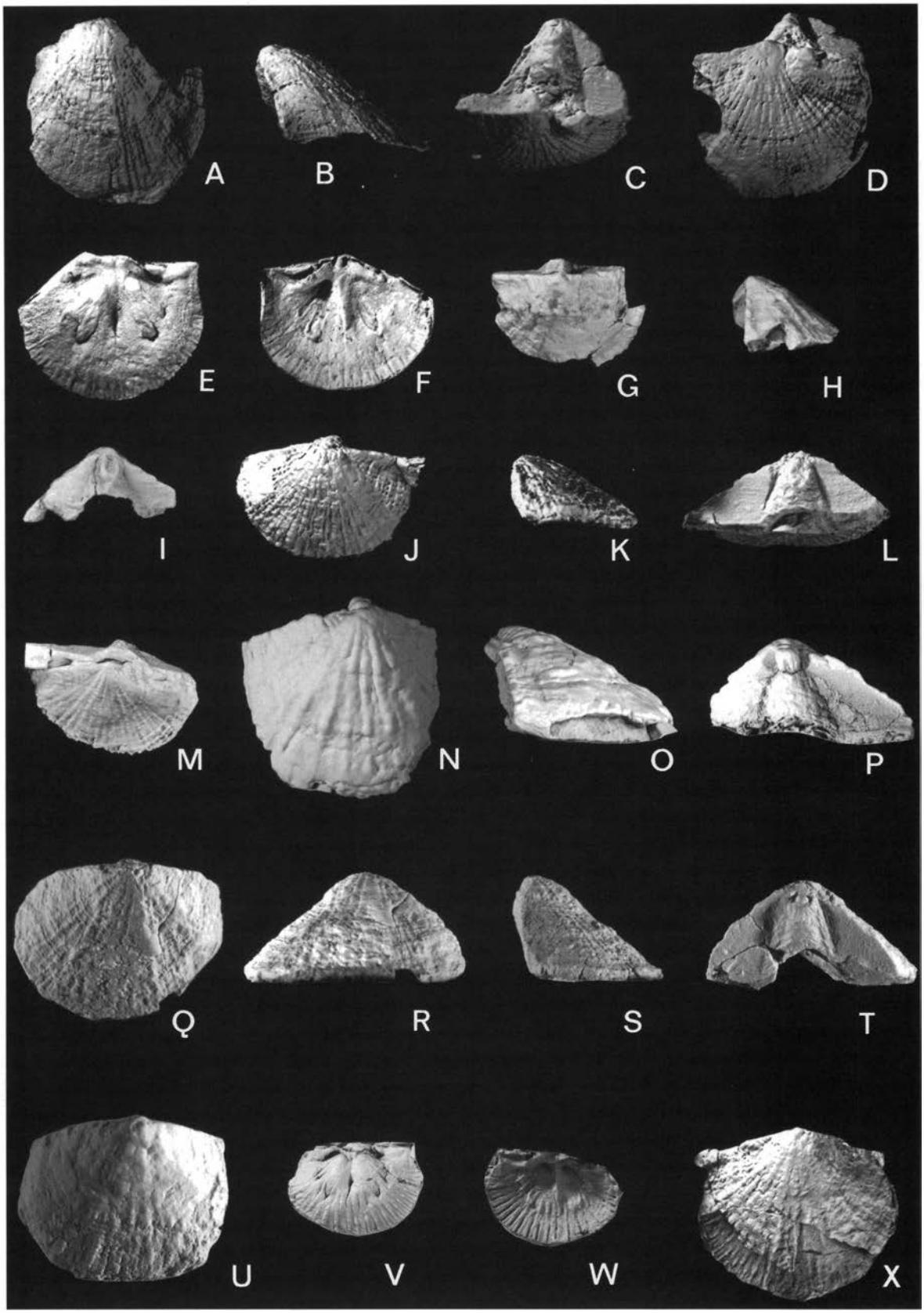


Fig. 5. A–D. *Kullervo* aff. *punctata*, PMO 162.070, ventral, lateral, posterior and dorsal view, Bratterud, Arnestad Formation, ×2. E. *Kullervo* aff. *punctata*, PMO 162.072, impression of the ventral interior, Bratterud, Arnestad Formation, ×2.2. F. *Kullervo* aff. *punctata*, PMO 162.072, latex cast, ×2.2. G–I. *Kullervo* aff. *lacunata*, PMO 162.083, ventral valve, Bratterud, Arnestad Formation, ×2.0. J–M. *Kullervo hibernica* Harper, 1952, PMO 162.085, ventral, lateral, posterior and dorsal view, Billingstad, Arnestad Formation, ×2.0. N–P. *Kullervo* aff. *lacunata*, PMO 162.086, ventral valve, Billingstad, Arnestad Formation, ×3.0. Q–T. *Kullervo* aff. *punctata*, PMO 162.065, ventral valve, Billingstad, Arnestad Formation, ×3.0. U. *Kullervo* aff. *punctata*, PMO 162.066, ventral valve, Billingstad, Arnestad Formation, ×3.0. V. *Kullervo* aff. *punctata*, PMO 162.067, impression of the dorsal interior, Billingstad, Arnestad Formation, ×2.0. W. *Kullervo* aff. *punctata*, PMO 162.067, latex cast, ×2.0. X. *Kullervo hibernica* Harper, 1952, PMO 162.088, ventral valve, Bratterud, Arnestad Formation, ×2.0.

Discussion. – *K. parva* was originally described by Cooper (1956) from the Effna and Edinburgh formations in Virginia, corresponding to the lower part of the *tvaerensis* conodont Biozone and middle part of the same Biozone, respectively (see Bergström 1990, fig. 17), USA. The anterior margin of these specimens is medianly invaginated, but not rounded as in the Norwegian specimen. Cooper (1956, p. 528) describes the pseudodeltidium as 'appearing as a vestige stage of that plate at the apex', which is nothing but the mere remains of the seal of the pedicle foramen, while the deltidium itself is broken off (see Cooper 1956, pl. 80, B, figs. 7–8).

The Norwegian specimens described here are affiliated with *K. parva* mostly because of the presence of similar sulcus in the dorsal valve, anteriorly drawn into short tongue, and ponderous cardinalia, and strong convexity of the dorsal valve.

K. aff. *parva* resembles *K. hibernica*, but the latter is easily distinguished from the former by its relatively wider shell, less concave sides, almost flat dorsal valve, more regular and less closely spaced ornamentation, short dorsal interarea with shorter umbonal chilidium, less deep dorsal sulcus, and by the strongly subapical foramen in the middle of a less convex deltidium. The subapical foramen described in one ventral valve (PMO 162.074) of *K.* aff. *parva* is a result of the sealing of the foramen, which has not grown entirely full in that case (Fig. 4S).

Kullervo aff. *punctata*

Figs. 5A–F, Q–T, V, W.

Material. – Two shells (PMO 162.070, L = 16.0, W = 15.0; PMO 162.072, L = 12.0, W = 15.0); nine ventral (PMO 162.065, L = 11.0, W = 16.0; PMO 162.066, L = 11.1, W = 14.5; PMO 162.105) and two dorsal valves of good to satisfactory preservation; eight moulds of the dorsal interiors (PMO 162.073, PMO 162.067).

Locality and horizon. – Bratterud, Arnestad Formation, just above big bentonite; Billingstad, Asker, Arnestad Formation, just below big bentonite; and from the Furuberget Formation (in the *Coelosphaeridium sphaericum* beds) at Fangberget (Ringsaker District) and Furuberget (Hamar–Nes District).

Description. – Shell fairly ventribiconvex, subquadrate in outline, some specimens clearly asymmetrical (PMO 162.065), 70–80% as long as wide with the maximum width along the hingeline to the mid-length. Anterior margin straight to rounded, in commissural plane rectimarginate. Cardinal extremities obtuse to gently acute. Sides broadly convex, gently concave postero-laterally.

Radial ribs weakly to well developed, bifurcating, with maximum of three branches, resulted in 8–9 ribs per 5 mm along the anterior margin. Number of primary ribs 8 up to 12.

The whole shell is covered with the concentric ridges. Frequency of the ridges per 5 mm of valve length, measured medianly anterior to 5 mm growth stage, is 10–16 in ventral valves and 14 in a dorsal valve.

Ventral valve pyramidal with slightly concave to gently convex shell surface in lateral profile. Ventral interarea high, triangular, nearly catacline to moderately apsacline, usually slightly concave in lateral profile becoming umbonally more apsacline, on average 50–80% as long as wide. Delthyrium about one-third as wide as the hingeline and about 65–80% as wide as long. Deltidium nearly flat to convex, projecting 0.9–1.8 mm away from the surface of interarea. Foramen small, always in the umbonal quarter of the deltidium, entirely apical or, in one specimen about 1.1 mm from apex (PMO 162.073), often sealed, on average with diameter of 1.5–1.7 mm.

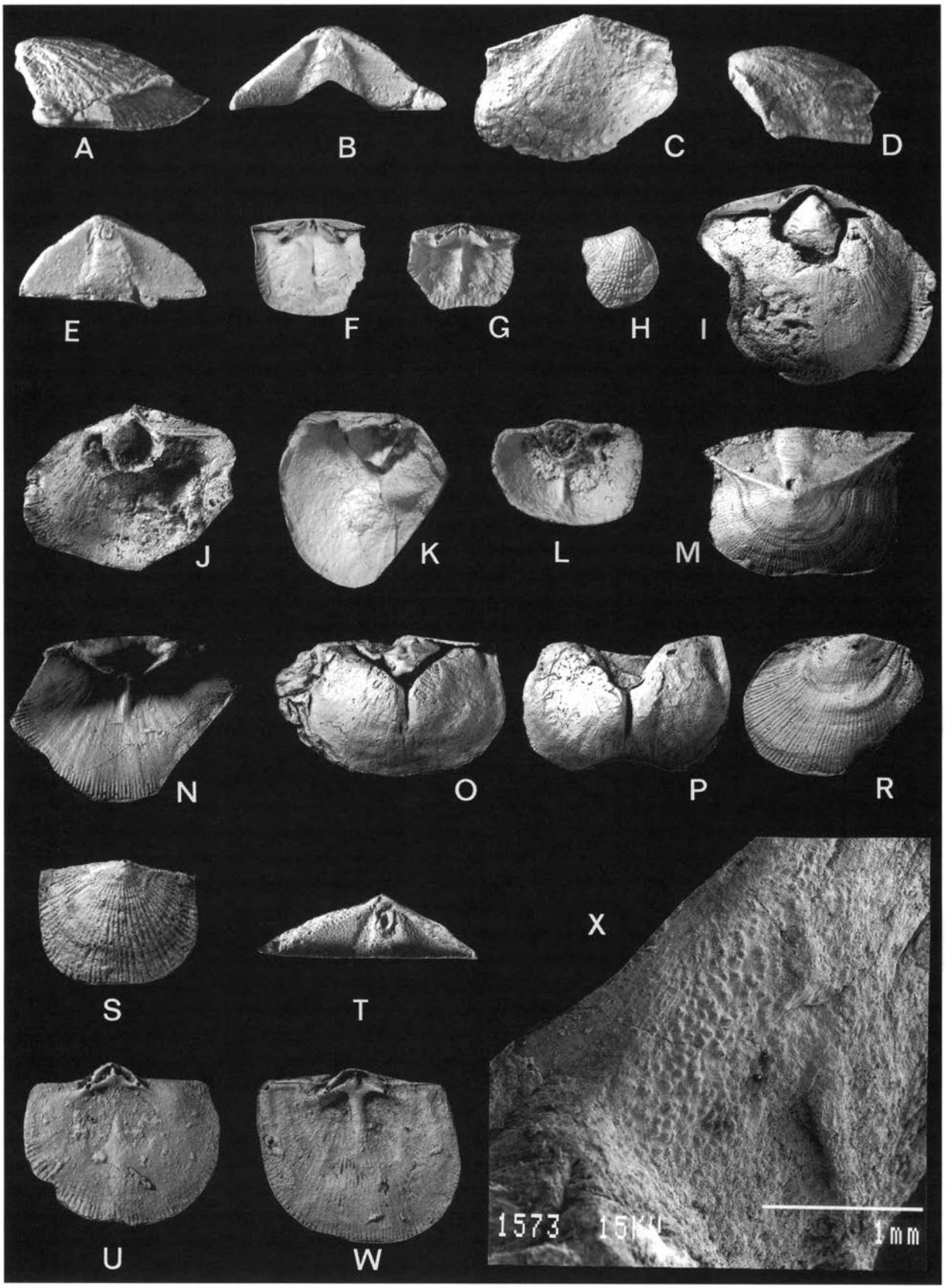
Dorsal surface gently convex in lateral and transverse profiles. Dorsal interarea moderately anacline, flat, chilidium convex.

Ventral interior with a spondylium triplex with hemisyrinx. Subspondylial lateral septa rudimentary, slender and low, reaching nearly to the anterior edge of the spondylium.

Cardinal process thin, plate-like, continuous with the chilidium. Socket walls divergent, about three times as wide as long, extending about half valve width, merge anteromedianly with the notothyrial platform. Median ridge well developed, wide, continuous with the notothyrial platform, but slightly lower, extending almost to margin of adductor field (see Fig. 5E). Notothyrial platform triangular. Adductor field subpetaloid, impressed on floor of the shell, extending to about valve mid-length or slightly anterior. The adductor scars gently divergent, slender, elongated, drop-shaped. Anterior pair of adductor scars larger than posterior pair, and twice as wide, strongly raised anteriorly. In one immature specimen (PMO 162.067) the anterior and posterior adductor scars of nearly equal size. It has also some fine, short, ray-like, radially arranged mantle canal tracks between the anterior adductor scars on both sides of the median ridge (Fig. 5, V, W). Weakly to well-developed marginal grooves, subparallel to valve margin.

Discussion. – The American type material from the Pratt Ferry Formation belong to the conodont Biozone of *Pygodus anserinus*. The described Norwegian specimens are affiliated to *K. punctata* on the basis of the ornamentation typical for this species, and almost straight cardinal extremities (cf. Cooper 1956). However, the Norwegian specimens have very variable exteriors, which differ from those of *K. punctata*, and rectimarginate anterior commissure instead of the emarginated one in the type material.

K. aff. *punctata* is similar to *K.* aff. *parva* (see above) with its relatively fine and equally developed pitted ornamentation. It differs from *K.* aff. *parva* in its rectimarginate anterior and lack of sulci in both valves, slightly coarser radial and concentric ornament, less convex lateral profile of both valves. The described species also has shorter and less acute cardinal extremities compared to *K.* aff.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parva. However, *K.* aff. *punctata* has an unexpectedly similar dorsal interior to that of *K. panderi*, with nearly identical shape of the adductor scars. Such an arrangement of the adductor muscle field was, up to now, known only in the stratigraphically older, Estonian *K. panderi*

Remarks. – One ventral valve (PMO 162.084), included in the species, differs from the rest of the specimens in its subcircular outline, more convex lateral profile of the ventral valve, wider delthyrium and bigger foramen. It also has rounded cardinal extremities and clearly unequal strength of radial ornamentation.

Kullervo cf. *lacunata*

Figs. 5G–I, N–P.

Material. – Two ventral valves (PMO 162.083; PMO 162.086, L = 8.0, W = 10.5, measurements taken at 8 mm growth stage) and one latex cast of the ventral exterior (original not preserved).

Locality and horizon. – Bratterud, Arnestad Formation, just above the big (Kinnekulle) bentonite; Arnestadtangen, Asker, Arnestad Formation; Billingstad, Asker; Arnestad Formation, just below big bentonite, Upper Ordovician.

Description. – Ventral valve subpentagonal in outline, about 60–80% as long as wide with the maximum width at hingeline. Anterior margin in younger growth stages straight, anterior commissure rectimarginate. Cardinal extremities gently acute to acute, sides posteriorly slightly concave.

Radial ribs strong, sparse, less developed in lateral regions, absent on cardinal extremities, bifurcating, branching twice, 4 costellae per 5 mm at 5 mm growth stage, measured medianly lateral. Number of primary ribs in umbonal area is 9.

Weak concentric ridges postero-laterally unequally developed, more continuous on the cardinal extremities and umbonally, nearly indistinguishable antero-medianly. Number of ridges per 5 mm of valve length, measured laterally anterior to the 5 mm growth stage, about 10.

Ventral valve pyramidal, with evenly flat surface and gently convex umbo in the lateral profile. Ventral interarea triangular, flat, apsacline, 90% as long as wide. Delthyrium about one-third as wide as the hingeline and about 90% as wide as long. Deltidium convex, projecting 1.2–1.7 mm away from the surface of interarea. Foramen moderate to large size, apical, with the diameter of 1.8–2.5 mm, surrounded by a small 1.0 mm high lip.

Discussion. – The specimen described by Alikhova (1969, p. 80, pl. V, fig. 2) from the Idaverean Stage of Valdai, Russia as *K. panderi* has ornament and outline that strongly resembles that of *K.* cf. *lacunata* from the Arnestad Formation of Oslo Region, but the latter could still be easily distinguished from the former by the presence of the elevated lip around the foramen. The described species resembles also the type material of *K. panderi* Öpik (1930, p. 234, pl. 19, fig. 228 pl. 21, fig. 260; Öpik 1934; pl. 35, figs. 1–5, pl. 37, fig. 2, text-figs. 37, 38, 39, 52) in having coarse, sparse radial ornamentation and the concentric ornamentation strongly developed and predominant only in the lateral regions.

The described species has also a relatively high ventral area and entirely apical foramen similar to that of *K. panderi*, but it could easily be distinguished from the latter by the less acute cardinal extremities, and the less impressed concentric ornamentation in the ventral lateral regions. It differs also by its smaller pedicle foramen and more irregular shape and slightly unequal strength of radial ribs. Orientation of the ventral interarea in *K. panderi* is catacline (Öpik 1934, p.169, text-fig. 39), rather than apsacline as in *K.* cf. *lacunata.*

Moderately acute cardinal extremities as in *K. aluverensis* Öpik (1934, pp. 172–173, pl. 38, fig. 1–1b, text-fig. 39, 53) and its general outline like *K.* cf. *lacunata*, but the latter has no subapical foramen in the middle of the deltidium, rather, an entirely apical pedicle foramen and also slightly thinner costellae than in *K. aluverensis.*

In outline, *K.* cf. *lacunata* also resembles *K. hibernica*,

Fig. 6. A–B. *Kullervo hibernica* Harper, 1952, PMO 162.088, ventral valve, lateral and posterior view, Bratterud, Arnestad Formation, ×2.0. C–E. *Kullervo hibernica* Harper, 1952, PMO 162.089, ventral valve, ventral, lateral and posterior view, Bratterud, Arnestad Formation, ×2.0. F. *Kullervo hibernica* Harper, 1952, PMO 162.090, impression of the dorsal interior, Arnestad, Arnestad Formation, ×2.0. G. *Kullervo hibernica* Harper, 1952, PMO 162.090, latex cast of the impression of the dorsal interior, ×2.0. H. *Hemipronites* ? sp. PMO 162.092, latex cast of the impression of the ventral exterior, Road section at Nydal-Furnes Church, Helskjer Member, Elnes Formation, ×1.5. I. *Clitambonites schmidti* Pahlen, 1877, PMO 162.093, impression of the ventral interior, from loose block, Rongstrand, probabaly *Coelosphaeridium-Mastropora* beds, Fossum Formation, ×1.2. J. *Clitambonites schmidti* Pahlen, 1877, PMO 162.093, latex cast, Fossum Formation, ×1.2. K. *Vellamo oandoensis?* Öpik, 1934, PMO 162.095, latex cast of the impression of the ventral interior, Bergevika, unit IV of the Mjøsa Limestone, ×1.5. L. *Vellamo oandoensis?* Öpik, 1934, PMO 162.096, latex cast of the impression of the ventral interior, Holetjern quarry SE part, lower part of the Mjøsa Limestone, ×1.5. M. *Clinambon anomalus* Schlotheim, 1822, PMO 162.097, latex cast of the impression of the ventral exterior, Gjøvik Kalkfabrikk, *Coelosphaeridium sphaericum* beds, Furuberget Formation, ×1.3. N. *Clinambon anomalus* Sclotheim, 1822, PMO 162.098, latex cast of the impression of the ventral interior, Tørud, *Coelosphaeridium sphaericum* beds, Furuberget Formation, ×1.3. O. *Ilmarinia dimorpha* Öpik, 1934, PMO 162.100, impression of the ventral interior, Fangberget, *Coelosphaeridium sphaericum* beds, Furuberget Formation, ×1.2. P. *Ilmarinia dimorpha* Öpik, 1934, PMO 162.099, impression of the ventral interior, Tørud, *Coelosphaeridium sphaericum* beds, Furuberget Formation, ×1.2. R. *Vellamo oandoensis* ? Öpik, 1934, PMO 162.104, latex cast of the impression of the ventral exterior, Bergevika North, unit V of the Mjøsa Limestone, ×1.5. S. *Vellamo oandoensis* Öpik, 1934, PMO 162.101, latex cast of the impression of the ventral exterior, ventral view, Bergevika North, unit V of the Mjøsa Limestone, ×1.3. T. *Vellamo oandoensis* Öpik, 1934, PMO 162.101, latex cast of the impression of the ventral exterior, posterior view, Bergevika North, unit V of the Mjøsa Limestone, ×1.3. U. *Vellamo oandoensis* Öpik, 1934, PMO 162.103, latex cast of the impression of the ventral interior, Bergevika North, unit V of the Mjøsa Limestone, ×1.8. W. *Vellamo oandoensis* Öpik, 1934, PMO 162.102, latex cast of the impression of the ventral interior, Bergevika North, unit V of the Mjøsa Limestone, ×1.8. *Kullervo* aff. *punctata*, PMO 162.106, SEM photo of the edge of spondylium, pseudopunctae and lateral septum, Billingstad, Arnestad Formation, ×29.

but it has an entirely different ornamentation on the ventral valve and less acute cardinal extremities.

Owen et al. (1990, p. 22) mentioned *Kullervo* cf. *lacunata* Öpik – determined by D.A.T. Harper – from the Arnestad Formation in the Oslo–Asker District. The described *K.* cf. *lacunata* resembles indeed *K. lacunata* Öpik (see Öpik 1934) in its extremely acute cardinal extremities. Therefore, the species identified by Harper as *K.* cf. *lacunata* is most likely conspecific with the material described here as *K.* cf. *lacunata.*

Family Clitambonitidae Winchell & Schuchert, 1895

Genus *Hemipronites* Pander, 1830

Hemipronites? sp.

Fig. 6H.

Material. – One mould of the ventral exterior (PMO 162.092).

Locality and horizon. – Road section at Nydal–Furnes Church (cf. Nikolaisen 1963, fig. 3) in the Helskjer Member of the Elnes Formation, early Llanvirn, as defined by Owen et al. (1990, p. 18). According to Owen et al. (1990, p. 18) the age is indicated as being late Kundan, in Baltic terms, Middle Ordovician.

Description. – Ventral valve transversely subquadrate in outline, slightly convex in lateral profile, with the maximum width at hingeline, and maximum height at about one-quarter of the valve length. Cardinal extremities slightly acute, anterior commissure with the shallow sulcus, and slightly emarginate anterior margin. Radial ribs bifurcating, on average 15 ribs per 5 mm along the anterior margin ventral valve. Ribs very fine, equally developed and evenly spaced. Concentric growth lamellae form a well-expressed imbricate sculpture.

Discussion. – The preservation state of the only Norwegian specimen available does not enable us to identify the genus without some doubt. However, the described specimen has been affiliated with *Hemipronites* (see Öpik 1934, pp. 96–98, pl. 42, figs. 1, 2; pl. 43, figs. 1a–b; text-figs. 12, 13.) because of its outline, imbricate sculpture and closely spaced fine radial ribs, all typical for the genus.

Genus *Clitambonites* Pander, 1830

Clitambonites schmidti Pahlen, 1877

Figs. 6I–J.

1877 *Orthisina schmidti* n.sp. – Pahlen, p. 23, pl. 2, figs. 5,6,7–9. 1930 *Clitambonites schmidti* (Pahlen) – Öpik, pp. 210–212, pl. 18, figs. 211–217; pl. 19, fig. 218; pl. 21, fig. 250. 1934 *Clitambonites schmidti* (Pahlen) – Öpik, pp. 83–89, pl. 3, figs. 1, 2; pls. 5–7; pl. 8, figs. 1, 2; pl. 10, fig. 1; text-figs, 8, 26, 33.

Material. – One mould of the ventral interior (PMO 162.093, L = >25, W = 35.0).

Locality and horizon. – One specimen (PMO 162.093) found in a loose block fallen from the top of the cliff at Rognstrand, Langesund–Skien District, probably from the *Coelosphaeridium – Mastopora* beds, Fossum Formation, Upper Ordovician.

Description. – Ventral valve transversely semielliptical in outline, convex in the lateral profile, with the maximum width about at mid-length of the valve. Cardinal extremities obtuse, the anterior margin rounded, commissure rectimarginate. Costellae of equal size, evenly spaced. Concentric growth lamellae, preserved on anterior of the specimen (PMO 162.093), forming a well-developed imbricate sculpture.

Ventral interarea short relative to length, flat and apsacline. Delthyrium as wide as long, less than half covered by convex deltidium. Foramen is not clearly observable in any specimen studied, possibly very small, sealed and entirely apical.

Ventral interior with wide, shallow spondylium, gently elevated anteriorly, supported medianly by short wide septum.

Discussion. – The described Norwegian specimens are assigned to the species *Clitambonites schmidti* on the basis of their ventral interior, ornament, deltidium and especially, the shape of spondylium, all typical for this species. In Estonia, this species has been found from the Aserian (C_{1a}) to Jöhvian Stages (D_1) (Öpik 1934).

Genus *Clinambon* Schuchert and Cooper, 1932

Clinambon anomalus Schlotheim, 1822

Figs. 6M, N.

1822 *Anomites anomala* n.sp. – Schlotheim, p. 65, pl. 14, figs. 2a–c. 1934 *Clinambon anomalus* (Schlotheim) – Öpik, pp. 118–124, pl. 1, figs. 3, 4; pl. 14, figs. 8, 8a–b; pl. 15; pl. 16, figs. 1,2,3; pl. 17, figs. 1, 1a–e; pl. 20, fig. 1; pl. 38, fig. 4; text-fig. 32.

Material. – One mould of the ventral exterior (PMO 162.097, L = 22.0, W = 30.0) and three moulds of the ventral interior (PMO 162.098).

Locality and horizon. – Found in the *Coelosphaeridium sphaericum* beds, Furuberget Formation, Upper Ordovician, in the localities Fangberget and Tørud in the Ringsaker District, and in a low road section S. of the old quarry at Gjøvik Kalkfabrikk, in the Toten District.

Description. – Ventral valve subquadrate in outline, with the maximum length at the hingeline, cardinal extremities acute, anterior margin straight and commissure gently uniplicate. Costellae of equal size, fine, evenly spaced.

Ventral interarea of medium length, flat, strongly procline. Delthyrium narrow, covered with the gently convex deltidium, pedicle foramen small, apical, oval, about with the diameter of 3 mm.

Ventral interior with the spondylium elevated anteriorly, supported medianly by septum half as long as valve. Adductor scars separated from diductors by invaginated sides of spondylium.

Discussion. – The described Norwegian specimens are assigned to *Clinambon anomalus* Schlotheim because of their species-characteristic profile, ornamentation and the ventral interior, and especially the shape of the spondylium. In Estonia, the species occurs in the interval from Jöhvi (D_1) to Oandu stage (D_3) (Öpik 1934).

Genus *Ilmarinia* Öpik, 1934

Ilmarinia dimorpha Öpik, 1934 Figs. 6O, P.

1934 *Ilmarinia dimorpha* n.sp. – Öpik, pp. 127–128, pl. 18, 40; text-fig. 26.

Material. – One mould of the ventral exterior and three moulds of the ventral interior (PMO 162.099, L = 22.0, W = 34.0; PMO 162.100, L = 26.0, W = 37.0).

Locality and horizon. – The two localities are in the *Coelosphaeridium sphaericum* beds, Furuberget Formation, Upper Ordovician, at Tørud and Fangberget in the Ringsaker District.

Description. – Ventral valve subquadrate in outline, strongly sulcate, with maximum length at the one-third length of valve, cardinal extremities obtuse, the anterior margin emarginate, commissure uniplicate. Ventral interarea of medium length, strongly procline. Delthyrium wide, slightly wider than long, about 60% as wide as the hingeline, covered by gently convex deltidium, foramen large, apical, suboval, about half as long as deltidium.

Ventral interior with the short spondylium, elevated anteriorly, supported medianly by septum. Sides of the spondylium slightly invaginated.

Discussion. – The described Norwegian specimens are assigned to the species *Ilmarinia dimorpha* (Öpik 1934, pp. 127–128, pl. XVIII, XL; text-fig. 26) because of their ventral sulcus, profile and the shape of spondylium, all typical for the species. The species was originally described by Öpik (1934) from the Oanduan Stage in Estonia.

Genus *Vellamo* Öpik, 1930

Vellamo oandoensis Öpik, 1934 Figs. 6K, L, R–U, W.

1934 *Vellamo oandoensis* n.sp. – Öpik, pp. 113–114, pl. 12, figs. 11a–14; pl. 30, figs. 1, 3; text-fig. 29.

Material. – Two moulds of the ventral exteriors (PMO 162.101, L = 19.0, W = 22.0; PMO 162.104), one ventral interior (PMO 162.094, L = 25.0, W = 25.0) and three moulds of the dorsal interiors (PMO 162.102, L = 18.0, W = 20.0; PMO 162.103, L = 17.0, W = 21.0). Probably two ventral interiors (PMO 162.095, L = 14.0, W = 19.0; PMO 162.096).

Locality and horizon. – Most of the material from the shore section at Bergevika N, in bed V, one in bed IV of Spjeldnæs 1982, Mjøsa Limestone. The rest of the material is from the same beds in the road section also of Bergevika N. (cf. Spjeldnæs 1982, fig. 3), Mjøsa Formation, Upper Ordovician. Two problematic ventral interiors from the lower part of the Mjøsa Formation in the quarry at Holetjern SE, in the Toten District.

Description. – Shell transversely semielliptical in outline. Anterior margin straight, in one specimen rounded. Cardinal extremities orthogonal to obtuse. Sides straight. Anterior commissure slightly sulcate.

Radial ornament bifurcating resulting in average seven ribs per 5 mm along the anterior margin ventral valve.

Ventral interarea short, flat and gently apsacline. Delthyrium narrow, slightly more than one-fourth as wide as the hingeline, covered entirely by convex deltidium. Foramen large, subapical, about two-thirds as long as the deltidium.

Dorsal valve subquadrate to semiovate, interarea anacline. Notothyrium covered by semicircular, convex chilidium. Dorsal interior with the plate-like cardinal process. Notothyrial platform nearly flush with dorsal interarea. Adductor field weakly impressed on floor of valve. Anterior pair of adductor scars almost equal size with posterior pair, median ridge weakly developed, extending to margin of adductor field, in one specimen confined to the umbonal region.

Discussion. – The described specimens have an outline and dorsal interior typical for the *V. oandoensis*. The Norwegian form also resembles *V. diversa* from America in its outline, but could be distinguished by its clearly less impressed dorsal adductor field and thinner dorsal valve (personal consultations with Mrs. Oive Tinn from Tartu). *V. oandoensis* was originally described by A. Öpik (1934) from the Oanduan Stage in Estonia, which is of approximately the same age as unit V of the Mjøsa Limestone in the Oslo Region (Spjeldnæs 1982). The other ventral moulds (PMO 162.104) (Fig. 6R) found in the same beds have finer radial ribs, 11 per 5 mm along the anterior, rounded anterior margin and strongly asymmetrical shell, different from that of *Vellamo oandoensis*. Two ventral

interiors (PMO 162.095; 192.096) (Fig. 6K, L) included here to *Vellamo* may also belong to *V. oandoensis.*

Paleobiogeography

There are many interesting palaeobiogeographic points regarding the clitambonitoids from the Upper Ordovician of the Oslo Region. The first concerns the distribution of the genus *Kullervo*, and the second the presence of typical East Baltic clitambonitoids in Norway.

In the central part of the Oslo Region (Oslo–Asker–Ringerike) the Atlantic Province assemblage occurs in beds around, and especially just above, the Kinnekulle Bentonite (of Bergström et al. 1995).

The great majority of the specimens of *Kullervo* are from above the level of bentonite, but, since the bentonite itself is missing (being washed out, or squeezed out tectonically) in the two localities where most of the specimens are found – Bratterud and the tunnel-roof at Billingstad – it cannot be excluded that the first occurrence of *Kullervo* in the Oslo Region is even below the bentonite. All the four species *K. hibernica, K.* aff. *parva, K.* aff. *punctata* and *K.* cf. *lacunata* have a range within the Arnestad and Furuberget formations of the Caradoc Series of Oslo Region.

This invasion of new genera, with a Baltic/American stamp in the Oslo Region was termed the Kukruse wave by Spjeldnæs (1978), based on the then current miscorrelation of the Norwegian beds with Estonian ones. Now the beds in question (upper part of the Arnestad Formation) correspond to Keila (from the upper part of the *D. multidens* Biozone to the lowest part of the *D. clingani* Biozone; see Männil, 1990) and perhaps latest Jõhvian stages (middle part of the *Diplograptus multidens* Biozone; see Männil & Meidla, 1994) of the Estonian chronostratigraphic scale (Fig. 2).

The genus *Kullervo* Öpik was originally described from Estonia, where it is part of the Middle Ordovician radiation of the clitambonitoids in this region (Öpik 1934, 1939). However, the earliest known occurrence of the genus is *Kullervo* sp. from Wales, a form resembling *K. complectens*, from the Middle part of Ffairfach Group in Llandeilo of Upper Llanvirn age (Lockley & Williams 1981), broadly equating with the uppermost *artus* to a level near the top of the *murchisoni* graptolite Biozones (Williams et al. 1972). That age is noteworthy, because it could indicate the time of migration of the first kullervoid from Baltica to Avalonia.

On the other hand, the first *Kullervo* in Estonia (*Glyptograptus teretiusculus* Biozone; see Männil & Meidla, 1994, chart 1) occurs shortly after the first occurrence of the genus in Wales and was probably derived independently from the last common ancestor of both the endemic Baltic species and pandemic Avalonian/American ones. Moreover, the oldest Estonian species, *K. lacunata*, has neither sulcus nor strongly pitted ornamentation, different from that of *K.* sp. from Wales. The oldest known records of gonambonitids are all from Baltica, there is nothing known about the gonambonitids from Avalonia predating the *K.* sp. and suitable for an ancestor of *Kullervo*, and so suggesting a Baltic species to be the descendants of an earlier Avalonian migrant.

In England, Wales and Ireland the genus has a range at least from the Llanvirn (Lockley & Williams 1981) to the Ashgill (Wright 1964, Hiller 1980). The Irish species *K. hibernica* was originally described from the Upper tuffs and shales in Grangegeeth of Caradoc age (Harper 1952). The occurrence of *K.* aff. *panderi,* the species resembles of *K.* aff. *punctata*, in the Derfel Limestone of N. Wales (Whittington & Williams 1955) is remarkable, especially because it occurs along with other brachiopods of the American assemblage mentioned below (such as *Palaeostrophomena* and *Sowerbyella*).

The Derfel Limestone is recently recognized as being Harnagian in age (see Zalasiewicz 1992, pp. 379–389). Because of the similarity in fauna, the Derfel Limestone may be correlated with the upper part of the Arnestad Formation in the Oslo Region, of supposed *peltifer* age, just above the rhyolitic Kinnekulle Bentonite.

In Estonia, several species have been found, in typical carbonate platform sediments, with low net sedimentation rates. The oldest known species of the genus in Estonia is *K. lacunata* from the Raasikuan Substage of Uhakuan Stage (C_{Ic}) (Röömusoks 1970). This level is close to the base of *Pygodus anserinus* Biozone (Männil & Meidla 1994). The ranges of the temporally next two species *K. panderi* and *K. intacta* are restricted to the lower part of the Kukruse Stage (C_{II}) (Röömusoks 1970). The stage is defined in the North Atlantic conodont succession as ranging from the upper part of the *Pygodus anserinus* Biozone to the lower part of *Prioniodus gerdae* subzone of the *Amorphognathus tvaerensis* Biozone, and in the graptolite succession it roughly corresponds to the interval of the *Nematograptus gracilis* Biozone (Männil 1986; Männil & Meidla 1994). *K. aluverensis* from the upper part of the Idaverean Stage (C_{III}) (Röömusoks 1970) corresponds to the interval represented by the lowermost part of the *Diplograptus multidens* Biozone (Männil & Meidla 1994), and is the youngest known occurrence of the *Kullervo* in Estonia, except for the possible occurrence of *K. complectens* in the Pirgu Stage (Öpik 1934). The stage corresponds to the upper part of the *Pleurograptus linearis* Biozone (Männil & Meidla 1994).

The three American species – *Kullervo parva, K. sulcata* and *K. punctata* were originally described (Cooper 1956) from formations which have been dated slightly older than Estonian stages named above (the corresponding Pratt Ferry, which was correlated with the Boutetout, Effna and Arline Formations by Cooper) and belong to the conodont Biozone of *Pygodus anserinus.* More recently, Bergström (1990) equated the lowest part of the Effna Formation with the lower part of the *tvaerensis* conodont Biozone and included the Boutetort and Edinburgh formations in the middle of that Biozone. The Pratt Ferry Formation was placed at a level low in the *anserinus* Biozone.

The Caradoc species *K. parva, K. ornata* and *K. sulcata*,

as well as the Ashgill *K. pyramidata* in America may have been derived from an earlier migrant from Avalonia, but they may also be of Avalonian origin.

Kullervo is found in the Atlantic Province of Jaanusson & Bergström (1980) of North America, and occurs there along with a number of brachiopod genera of possible Baltic origin, such as *Palaeostrophomena, Christiania, Sowerbyella, Diambonia* and *Bilobia* as well as genera of less specific, possibly American origin, such as *Ptychoglyptus, Anisopleurella* and *Cyphomena* (Jaanusson & Bergström 1980).

This assemblage is unknown in the Mid-Continent part of North America, but recurs (without reports of *Kullervo*) in the westernmost part of North America, where it belongs to terrains or platelets added to North America after the Ordovician (Potter et al. 1980).

The picture that emerges from *Kullervo* is that they may have had two diversification centres; one in Avalonia and the other in Baltica, where they evolved in parallel from a common early kullervoid ancestor. That early kullervo or the last common ancestor for both the endemic species of Baltica and the Avalonian/American ones may have been migrated from Baltica to Avalonia or evolved there already by the Early Llanvirn. During the Late Llanvirn, the *Kullervo* (*K.* sp and/or its descendants; see Lockley & Williams 1981) probably migrated from Avalonia to North America, and finally settled again in Baltica (Oslo Region; *K. hibernica*, and probably also *Kullervo* aff. *punctata* and *Kullervo* aff. *parva*) in the time of the big bentonites. The distinct "Baltic" species *K. complectens* shares the similar outline and ventral muscle field with *K. complectens albida* (Caradoc/Ashgill, Avalonia) and the *K. pyramidata* (Ashgill, North America, see Cooper & Kindle 1936) and its occurrence in the Ashgill of Baltoscandia (see above) may indicate that it was a migrant from American/Avalonian.

However, it cannot be excluded that the migration was in the opposite direction, from Baltica to Avalonia in late Llanvirn. Thus, some Baltic *Kullervo* may be found in Avalonia. On the other hand, by the time in question the endemic Baltic species were probably already highly adapted to the specific habitat on the Baltic carbonate platform, so they should have had low migration potential.

The paleobiogeography and ecology of the other clitambonitoids found in the Oslo Region is different from that of the almost cosmopolitan *Kullervo. Clinambon, Ilmarina* and partly *Clitambonites* are otherwise endemics to the Baltic carbonate platform. *Vellamo* has a world-wide distribution, but also mostly in carbonate platforms. In the Oslo Region they are found in the northern and western districts of the region, which are well known for their Baltic fauna (Holtedahl 1909; Størmer 1953).

The precise correlation of the beds in these districts (Mjøsa, Skien–Langesund and Hadeland) is not well developed, and the presence of Baltic species and genera is generally taken as an indication of the same age as in Estonia (it was a mistake with *Kullervo* in the Oslo–Asker and Ringerike Districts, and caused some doubt regarding correlation also in the other districts).

With few graptolites, and without a well-established conodont stratigraphy in these districts, it is difficult to use both the clitambonitoids and other conventional fossils such as trilobites and brachiopods, because we do not know if they are part of the faunal area of the Baltic Platform, or if they have a distribution and migration pattern similar to that seen in *Kullervo*.

The main reason for this doubt is that in the Oslo Region the genera in question (*Clinambon, Clitambonites, Ilmarina* and *Vellamo*) occur in sediments strikingly different from those in Estonia and Sweden. In the carbonate platform areas, their enclosing carbonate, partly with a slight clay content, shows a low net sedimentation rate. In Norway, the same genera occur in rapidly sedimented silt-clay-carbonate rocks which not only look different, but also indicate strikingly different bottom conditions as well as sedimentation rates.

On the other hand, *Clitambonites, Ilmarinia, Clinambon* and *Vellamo* from the silt-clay carbonate rocks of the Oslo Region are not found in the shales where the *Kullervo* occurs, and vice versa. These two different assemblages are presumed to reflect neither different ages nor geographical distances, but the different ecology of *Kullervo* as compared with the rest of Middle and Upper Ordovician clitambonitoids in Baltica. However, the differences in water depth and especially in the bottom conditions between the shale facies of foreland basin and the silt-clay-carbonate rock facies of the slope of the carbonate platform may have played a big part in the separation of clitambonitoids in the Oslo Region.

Since modern benthic invertebrates are generally very sensitive to changes in substrate and sedimentation rate, it is difficult to refer the Norwegian material to Estonian species without some doubt. In Estonia, *Clinambon anomalus* occurs in both the clay-marls and limestones, indicating low rather than high sensitivity of the species there in this respect. However, the subspecies in the Oslo Region could be different from those described by Öpik in Estonia (see Öpik 1934).

The present samples are too small to resolve this problem on the species level, and can therefore only help to ascertain the presence of the genera, and the palaeobiogeographic relationships the Baltic Carbonate Platform and the Oslo Region.

Acknowledgements. – We record with pleasure the helpful comments received from Professor M. Rubel, who read the manuscript, and Mrs. O. Tinn, who helped to identify the species of *Vellamo*. We also thank Dr. A. W. Owen, Dr. G. Baarlie and Dr. A. D. Wright for comments on the manuscript. Vinn is indebted to the Research Council of Norway for a grant in support of the study of Baltoscandian clitambonitoid brachiopods in Oslo and to the Estonian Science Foundation (grant ETF 3274) for financial support.

Manuscript received February 1997

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