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THE ORDOVICIAN CLITAMBONITIDINE BRACHIOPOD GENUS *VELLAMO* IN ESTONIA

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Abstract. *Vellamo* Öpik, 1930 is a cosmopolitan Ordovician brachiopod genus originating from the epicontinental seas of the Baltoscandian Palaeobasin. As a result of the systematic revision of the Estonian material, 16 *Vellamo* species are described or discussed. The morphological characters of taxa are presented. Special attention is paid to the ontogenetical changes in the shell morphology, as the earliest growth stages are closely similar in all species of the genus. On the basis of the stratigraphical distribution three successive stages in the development of the Estonian species are distinguished.

Key words: Ordovician, clitambonitidine brachiopods, morphology, stratigraphy.

INTRODUCTION

The genus *Vellamo* Öpik, 1930 with more than 30 species, has a wide geographical distribution. It has been recorded from the East European Platform, the British Isles, North America, western slope of the Ural Mountains and possibly from Algeria, Belgium, and Tasmania. Sixteen species have been reported from Estonia, Ingria (St Petersburg region of Russia), and Podolia. The northwestern part of the East European Platform is very likely the origination area of the genus ranging here from the Llanvirn up to the end of the Ordovician.

The studied Estonian collections include nearly 800 well-preserved specimens from 65 outcrops and 6 drillcores (Figure). The character list of 16 *Vellamo* species (Table 1) has been compiled for the present study, based on the emended diagnoses (given in this paper) or original diagnoses. Data matrix shows high variability of certain species, which can be explained with the different growth stages and natural intraspecific variability.

The described specimens are housed in the Museum of the Institute of Geology, University of Tartu (TUG), Institute of Geology at Tallinn Technical

University (IGT), and Estonian Museum of Natural History (MNH). The studied material comprises all holotypes of the *Vellamo* species of Öpik (1930a), except for *Vellamo viruana* Öpik, 1930, whose holotype is presumably lost.

HISTORY OF STUDY

The first species of *Vellamo* was described by Eichwald as *Orthis verneuilii* in 1841. Pahlen (1877) described *Orthisina pyramidalis* and a subspecies *Orthisina verneuilii wesenbergiensis*.

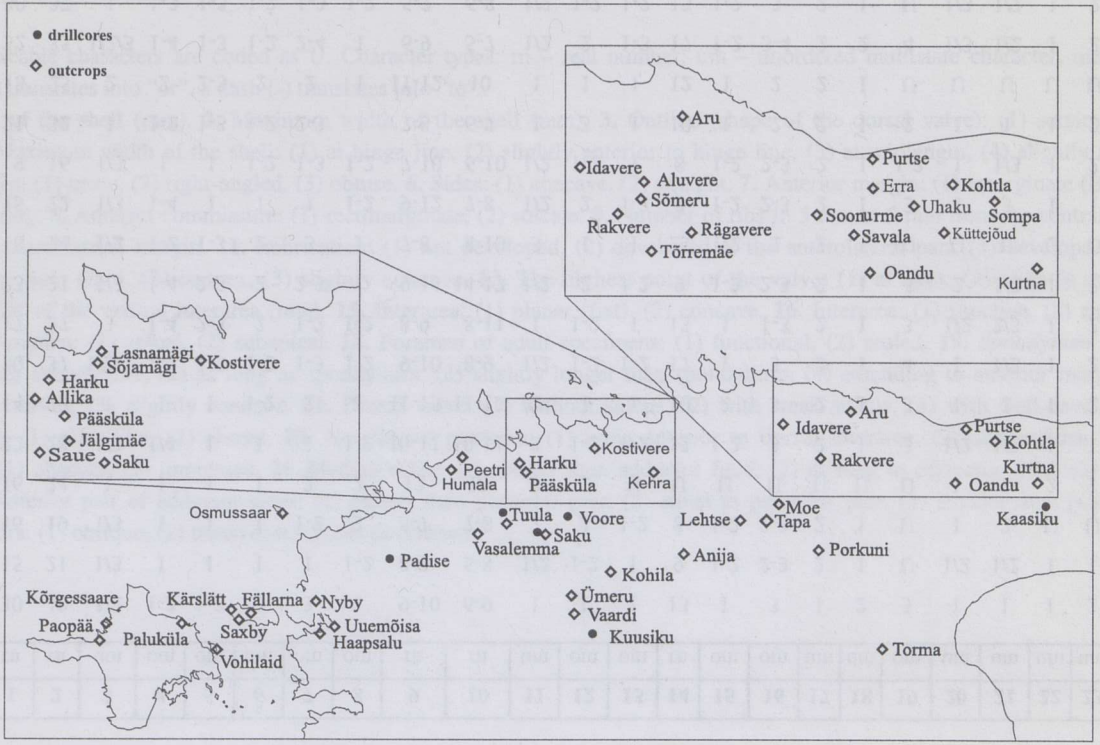
Öpik erected *Vellamo* as a new subgenus of the genus *Clitambonites* Pander, 1830 (Öpik, 1930a), noting a high interarea, fine costellation, and strong chilidium. He assigned six East Baltic species to the genus: *Orthisina trigonula* Eichwald, *O. pyramidalis* Pahlen, *O. complectens* Wiman, *O. emarginata* Pahlen, *Orthis verneuilii* Eichwald, and *O. sinuata* Pahlen. Also three British species – *Skenidium*? *Shallockiense* Davidson (considered by him as a synonym of *Clitambonites* (*Vellamo*) *pyramidalis* (Pahlen)), *C. complectens* (Wiman) var. *albida* Reed, and *O. adscendens* Davidson, *non* Pander; and two American species – *C. diversus* (Shaler) and *C. rogerensis* Foerste were regarded as belonging to the genus in the same work.

Öpik (1930a) described also two new *Vellamo* species: *Clitambonites* (*Vellamo*) *parvus* and *C.* (*V.*) *ultimus*. In a different paper (Öpik, 1930b) another new species, *C.* (*V.*) *viruanus*, was erected, based on a single ventral valve.

Schuchert and Cooper (1932) who regarded *Vellamo* in the rank of a genus mentioned that it differs from *Clitambonites* in important details (position of the interarea, sculpture of the surface, shape of the spondylium). As to phylogeny of the clitambonitidine taxa, the authors regarded *Apomatella*, *Pahlenella*, and *Vellamo* as sister groups, and the genus *Clinambon* as having its roots in *Vellamo*. They noted the European origin of the superfamily *Clitambonitacea* and its later expansion to North America. Seven American species, 11 European species, and 5 subspecies were listed in the genus.

Öpik (1934) gave a 10-point collation of the genera *Clitambonites* Pander and *Vellamo* Öpik. The absence of imbrication, flat or slightly convex dorsal valve, large foramen, high ventral interarea, *spondylium simplex*, and the asymmetry of the ventral valve were pointed out for *Vellamo*. That work comprised a thorough review of morphology and the description of 19 species and subspecies; 12 of them were new. Three species, assigned in his previous paper (Öpik, 1930a) to *Vellamo*, were transferred to other genera: *Pahlenella trigonula* (Eichwald), *Kullervo complectens* (Wiman), and *Ilmarinia sinuata* (Pahlen). The phylogenetic scheme was given, showing a common ancestor with *Apomatella*, *Ilmarinia*, and *Clinambon*.

In the early 1950s D. Kaljo summarized his research on *Vellamo*. The manuscript is deposited at the Institute of Geology, University of Tartu (Kaljo, 1951).



Distribution of drillcores and outcrops mentioned in the text.

Table 1

Character state matrix used for taxonomic descriptions

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
	rn	rn	um	om	om	om	om	om	rn	rn	um	om	om	rn	om	om	um	um	om	um	um	um	um	um	om	um	um
V. aenigma	30	40	1/2	1-2	1-2	2	3	1	9-10	6-9	1	1	1	13	1	3	1	2	3	1	1	1	2	2	3	2	1
V. ambisulcata	15	21	1/3	1	1	1	1	1-2	8-9	5-8	1/2	1-2	1	9	1-2	2-3	2	1	U	1/2	1/2	1	1	2	1	2/3	1
V. anijana	16	19	1/3	1	1	1	1-2	2	5-7	7-8	2	2	1-2	8	1-2	2-3	2	1	U	1	2	U	U	U	U	U	U
V. defecta	16	24	1	1	1	1	2	2	12	10	2	U	U	U	U	U	U	U	U	1	3	2	1	1	1	U	3
V. emarginata	22	28	1/3	1/4	1	1	1	1-2	10-11	10-11	2	1-2	1-2	12	1-2	3	2	1	3	1/2	1/2	1	1	2	2	U	3
V. leigeri	14	20	1	1	1	1-2	2	1	11-13	11-13	2	2	1	10	2	3	2	1	3	1	2	1	2	1	1	U	3
V. magna	30	37	1/2/3	1-3	1-3	1-2	1-3	1-2	9-10	8-9	1/2	1-2	1-2	17	1	3	2	1	4	1	1/2	1	2	2	2	2	2/3
V. oandoensis	17	27	3	1-4	2-3	2	1-2	1-2	8-9	8-11	1	1-2	1	13	1	1-3	2	1	3	1/2	2/3	1	2	1	2	2	2/3
V. parva	23	21	1/3	1-4	2-3	2	2-3	1	9-15	14-17	1/2	2	1-2	9	1-2	2-3	2	1	3	2	1/2	1	2	1	1-2	3	1/3
V. phrygia	18	24	1/2	1-2	1-3	2	3	1	7-8	8-10	3	1	1	25	1-2	2	2	1	U	U	U	U	U	U	U	U	U
V. praeemarginata	15	22	1/3	1-4	1	1	1	1-2	9-12	7-8	1/2	2	1-2	8	1-2	2-3	2	1	3	1	3	1	1	2	2	3	2
V. pyramidalis	9	16	1/3	1	1	1-2	1-3	1-2	7-10	6-10	1/2	1-2	1	8	1-2	2-3	2	1	1-2	1	1/3	1	2	2	1-2	1/2	2
V. silurica	21	32	1	1-2	1-3	1-2	2-3	1	7-8	6-7	1	3	1	10	1	2	2	1	2	1	1	1	2	2	1	U	3
V. symmetrica	18	25	2	2	2-3	2	2	1	11-12	10	1	1	1	12	1	2	2	1	U	U	U	U	U	U	U	U	U
V. verneuilii	32	35	1/2/3	1-4	1-3	1-2	2-4	1	6-9	5-7	1/2	2	1-3	17	1-2	3-4	2	2	4	1/3	1/2	1	2	2	2-3	2/3	2
V. wesenbergiensis	30	37	1	1-3	1-3	1-2	1-3	1-2	5-7	6-8	1/2	1-2	1-2	13	1-2	3	2	1	U	1/3	1/2	1	2	2	1-2	3	2/3

Unknown or unapplicable characters are coded as U. Character types: rn – real number, um – unordered multistate character, om – ordered multistate character. A slash (/) translates into "or", a dash (-) translates into "to".

1. Maximum length of the shell (mm). **2.** Maximum width of the shell (mm). **3.** Outline (shape of the dorsal valve): (1) semiovate, (2) semicircular, (3) subquadrate. **4.** Maximum width of the shell: (1) at hinge line, (2) slightly anterior to hinge line, (3) at midlength, (4) slightly anterior to midlength. **5.** Cardinal extremities: (1) acute, (2) right-angled, (3) obtuse. **6.** Sides: (1) concave, (2) straight. **7.** Anterior margin: (1) emarginate (B-shaped), (2) straight, (3) rounded, (4) bulging. **8.** Anterior commissure: (1) rectimarginate, (2) sulcate. **9.** Number of ribs in 5 mm at 5 mm from the ventral beak. **10.** Number of ribs in 5 mm at the anterolateral margin. **11.** Imbrication: (1) not developed, (2) developed at the anterolateral part, (3) developed all over the surface. **12.** Ventral valve: (1) plain (flat), (2) convex, (3) slightly concave. **13.** The highest point of the valve: (1) at apex, (2) slightly anterior to apex, (3) at midlength. **14.** Height of the ventral interarea (mm). **15.** Interarea: (1) planar (flat), (2) concave. **16.** Interarea: (1) procline, (2) catacline, (3) apsacline, (4) orthocline. **17.** Foramen: (1) apical, (2) subapical. **18.** Foramen of adult specimens: (1) functional, (2) sealed. **19.** *Spondylium simplex* supported by ridge: (1) shorter than spondylium, (2) as long as spondylium, (3) slightly longer than spondylium, (4) extending to anterior margin. **20.** Dorsal valve: (1) flat, (2) slightly convex, (3) slightly concave. **21.** Dorsal valve: (1) without sulcus, (2) with weak sulcus, (3) with well-developed median sulcus. **22.** Cardinal process: (1) plate-like, (2) absent. **23.** Notothyrial platform: (1) lying anterior to dorsal interarea, (2) nearly flush with dorsal interarea. **24.** Adductor field: (1) obscure, (2) impressed. **25.** Median ridge: (1) shorter than adductor field, (2) as long as adductor field, (3) extending anterior to adductor field. **26.** Anterior pair of adductor scars: (1) greater than posterior pair, (2) equal to posterior pair, (3) smaller than posterior pair. **27.** Ridge between adductor scars: (1) oblique, (2) transverse, (3) not developed.

PLATE I

Figs. 1, 2, 5. *Vellamo verneuilii* (Eichwald, 1841). Neotype. Ventral valve IGT Br 477. Kõrgessaare, Vormsi Stage. Interior, exterior, and lateral views. Showing orthocline ventral interarea. The space under spondylium and the apical part of the spondylium are filled with the secondary shell material. × 1.5.

Figs. 3, 4, 6, 9, 13. *Vellamo verneuilii* (Eichwald, 1841). Complete shell TUG 73/152. Kõrgessaare, Vormsi Stage. Lateral, anterior, ventral, posterior, and dorsal views. Showing subapical sealed foramen. × 1.5.

Fig. 7. *Vellamo verneuilii* (Eichwald, 1841). Dorsal valve IGT Br 476. *Sine loco*. Interior view. Showing bulging anterior margin. × 1.5.

Figs. 8, 10, 12. *Vellamo verneuilii* (Eichwald, 1841). Ventral valve IGT Br 925. Kõrgessaare, Vormsi Stage. Lateral, exterior, and interior views. Showing subapical sealed foramen and unusual subcircular outline. × 1.5.

Fig. 11. *Vellamo verneuilii* (Eichwald, 1841). IGT Br 480. Kõrgessaare, Vormsi Stage. Dorsal valve, interior view. × 1.5.

Figs. 14–16. *Vellamo leigeri* Öpik, 1934. IGT Br 483. Paluküla, Vormsi Stage. Dorsal and ventral valves. × 2.

PLATE II

Figs. 1, 2, 4, 5. *Vellamo praeemarginata* Alichova, 1953. Ventral valve TUG 892/2. Aluvere, Haljala Stage. Interior, posterior, lateral, and ventral views. × 1.5.

Figs. 3, 6. *Vellamo ambisulcata* Öpik, 1934. Dorsal valve IGT Br 504. Rakvere, Keila Stage. Interior and exterior views. × 1.5.

Figs. 7, 10, 13, 16, 17. *Vellamo emarginata* (Pahlen, 1877). Neotype. Complete shell with several bryozoan colonies TUG 72/148. Oandu, Keila Stage. Lateral, exterior, posterior, dorsal, and anterior views. × 1.5.

Figs. 8, 9, 11, 12, 14. *Vellamo ambisulcata* Öpik, 1934. Holotype. Complete shell IGT Br 502. Rakvere, Keila Stage. Dorsal, anterior, posterior, ventral, and lateral views. × 2.

Figs. 15, 18. *Vellamo emarginata* (Pahlen, 1877). Dorsal valve TUG 74/147. Oandu, Keila Stage. Interior and exterior views. × 2.

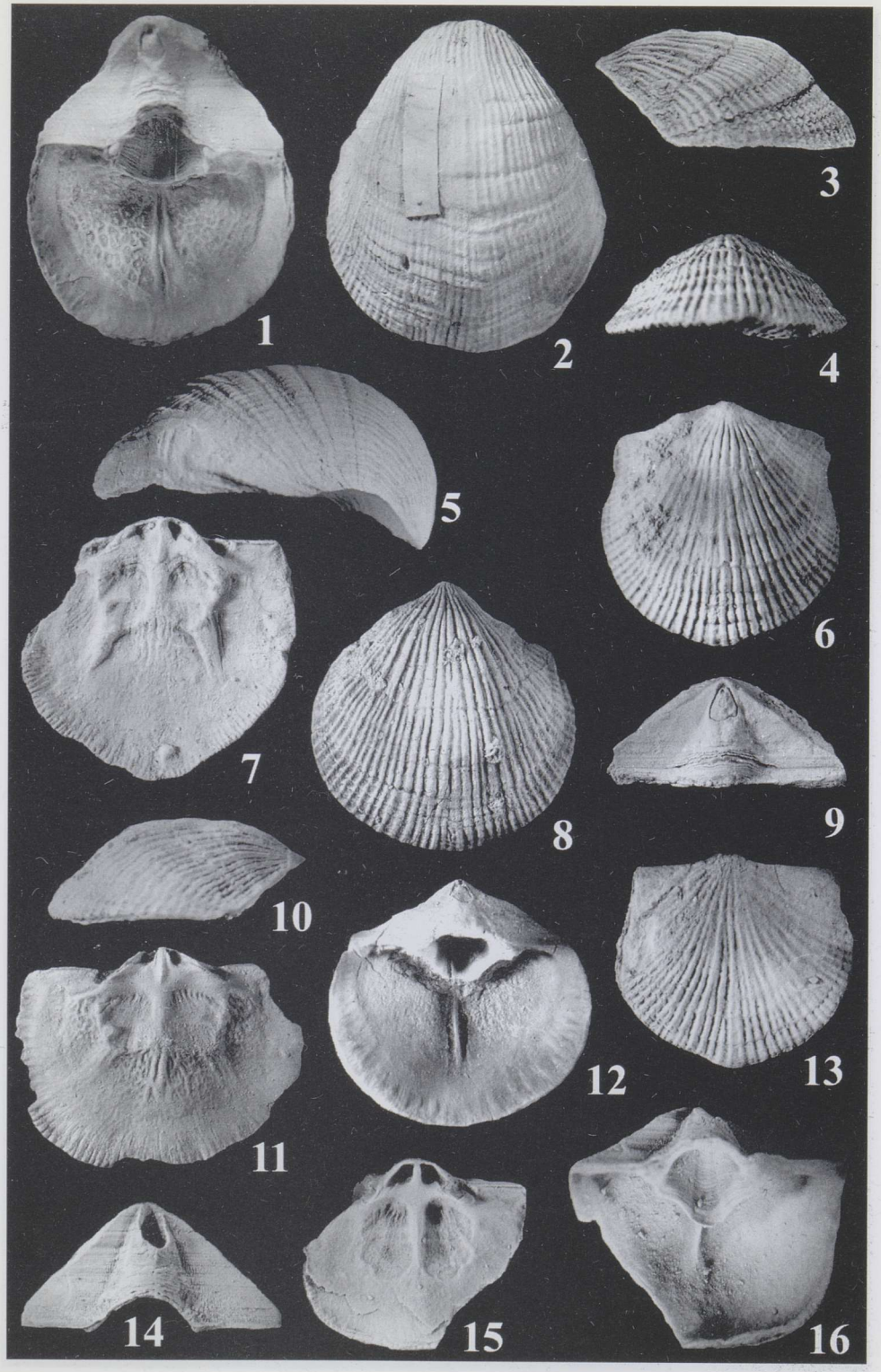
PLATE III

Figs. 1–4, 6. *Vellamo pyramidalis* (Pahlen, 1877). Complete shell IGT Br 511. Kohtla, Kukruse Stage. Figured by Öpik (1934, pl. 11, figs. 3a,b) as *Vellamo simplex* Öpik. Posterior, lateral, dorsal, anterior, and exterior views. × 4.

Figs. 5, 7–10. *Vellamo pyramidalis* (Pahlen, 1877). Neotype. Ventral valve TUG 39/76. Kohtla, Kukruse Stage. Showing twisting of the ventral apex. Lateral, posterior, interior, exterior, and anterior views. × 4.

Figs. 11, 13. *Vellamo pyramidalis* (Pahlen, 1877). Dorsal valve IGT Br 513. Kohtla, Kukruse Stage. Exterior and interior views. × 3.

Figs. 12, 14–16. *Vellamo anijana* Öpik, 1934. Holotype. Complete shell IGT Br 510. Anija, Haljala Stage. Posterior, exterior, anterior, and dorsal views. × 3.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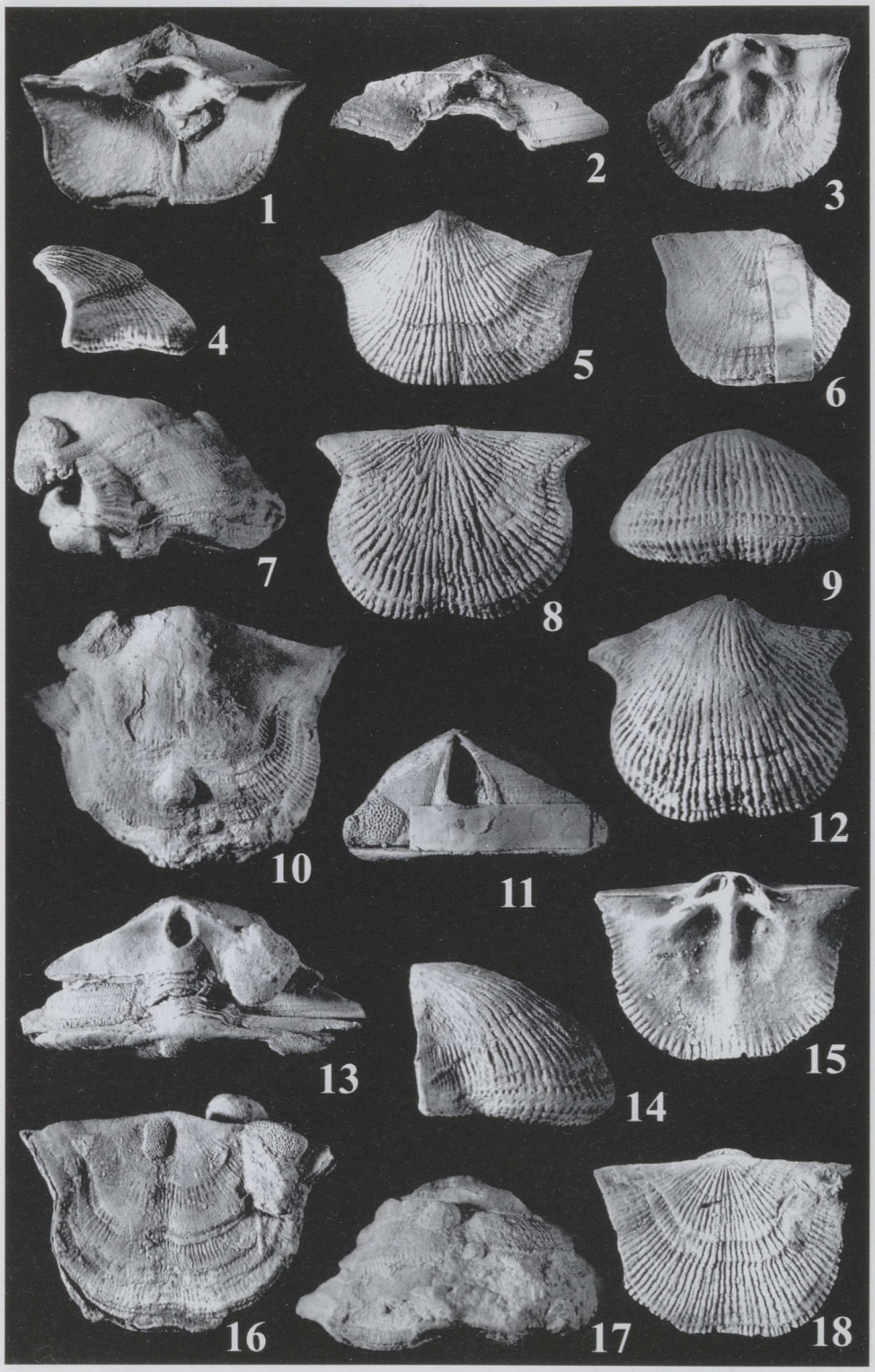

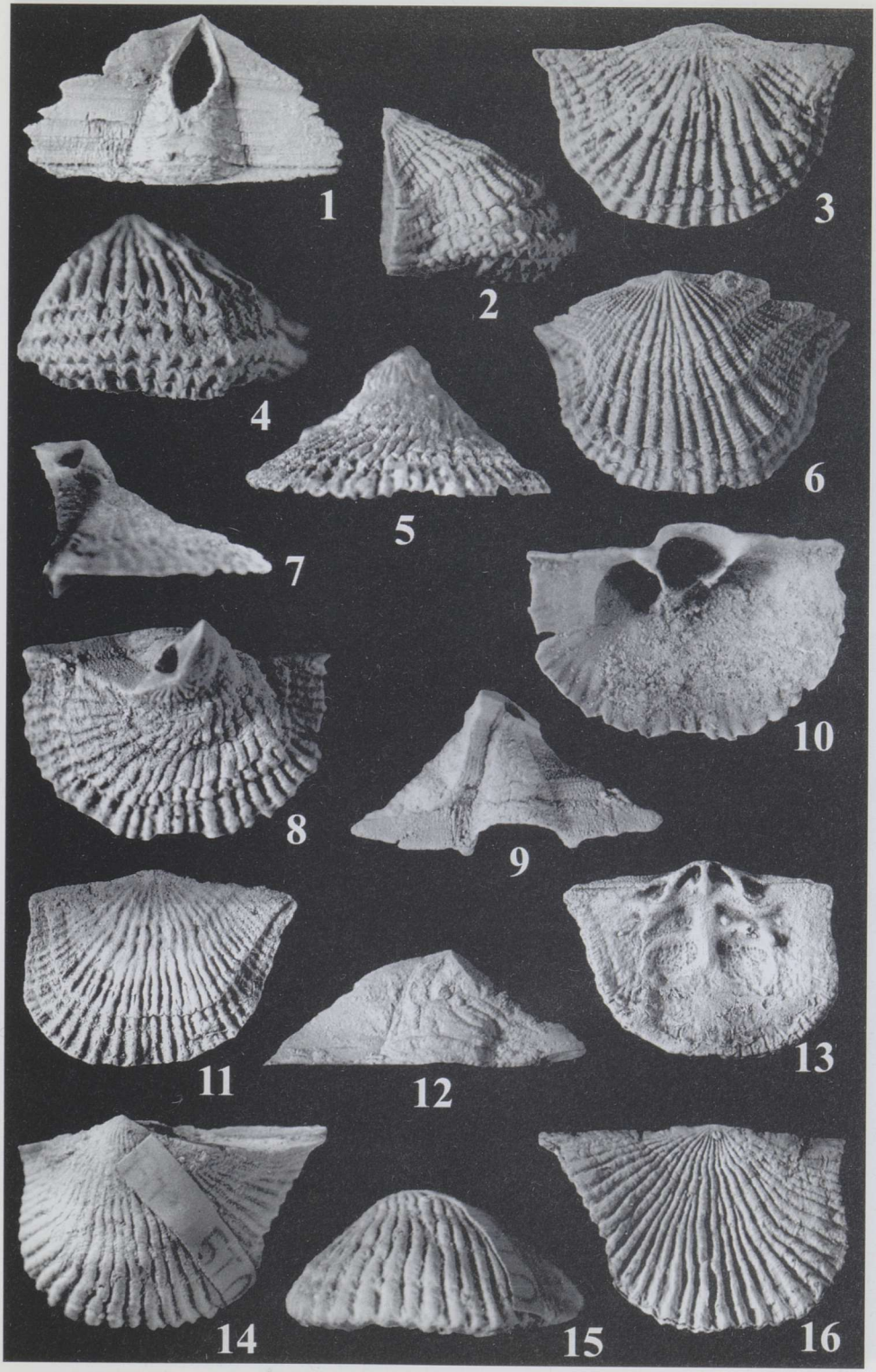
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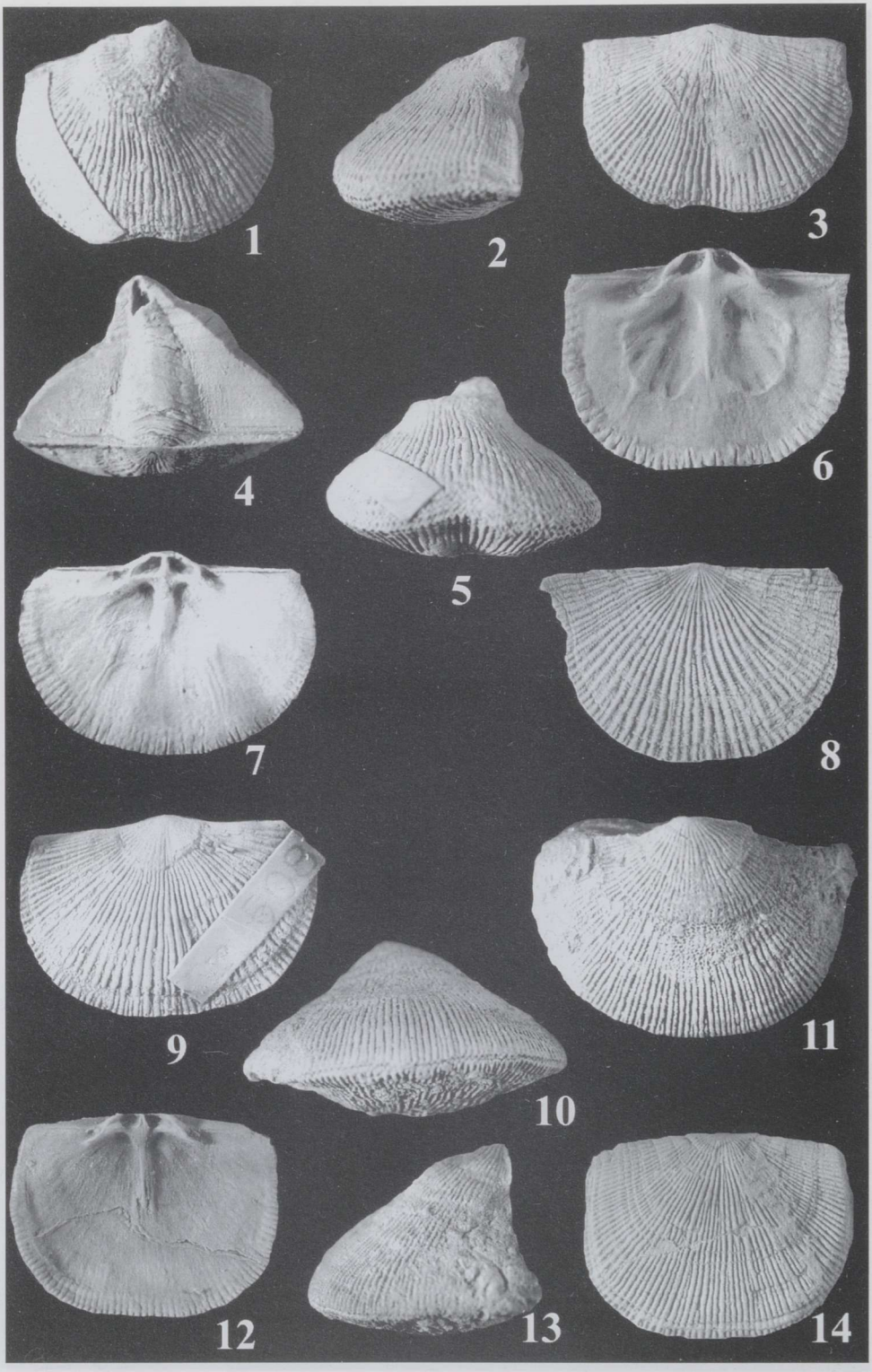

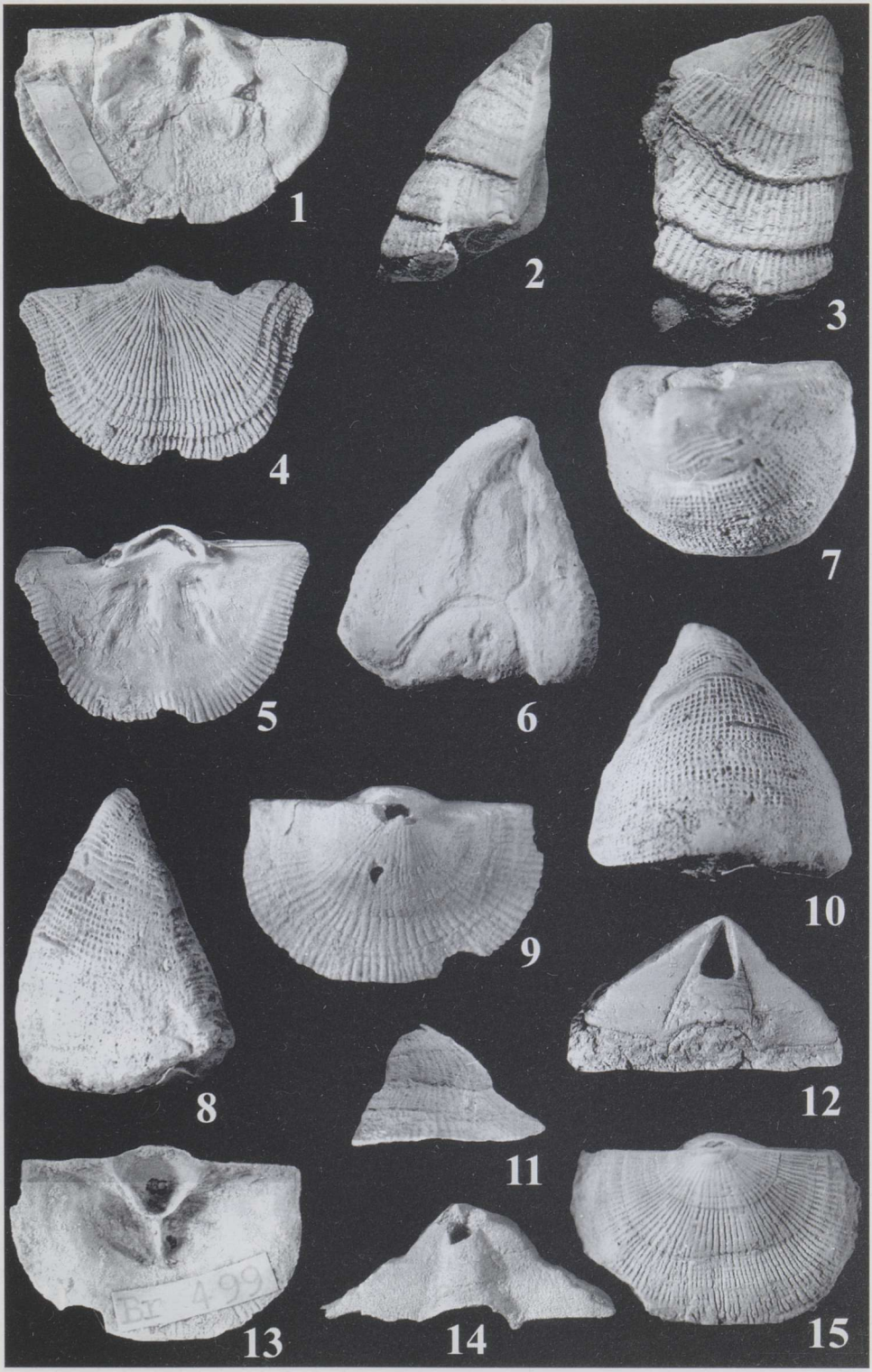
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PLATE VI

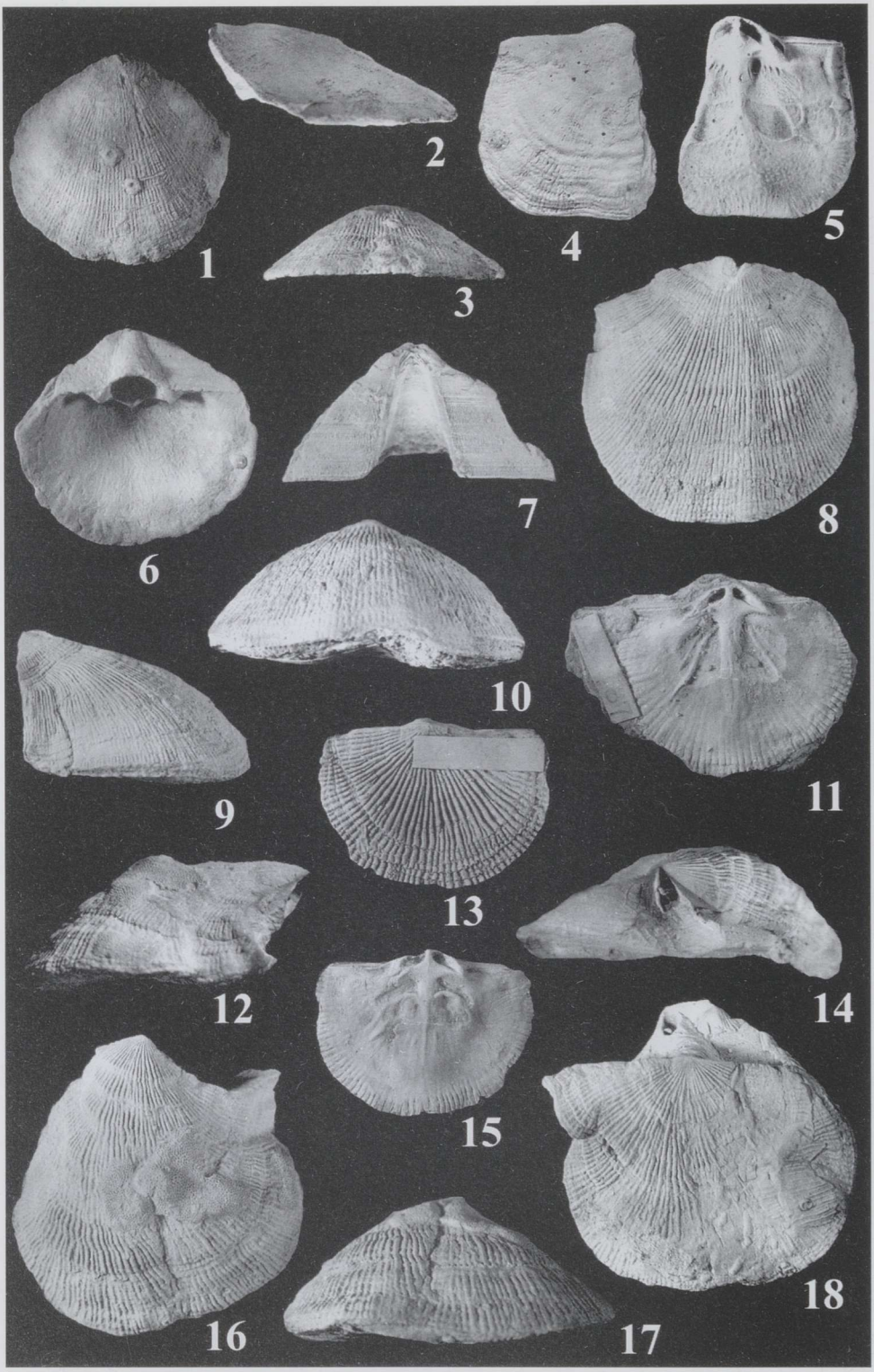


PLATE IV

Figs. 1–5. *Vellamo oandoensis* Öpik, 1934. Holotype. Complete shell IGT Br 505. *Sine loco*, Oandu Stage. Exterior, posterior, lateral, dorsal, and anterior views. × 2.

Figs. 6, 8. *Vellamo oandoensis* Öpik, 1934. Dorsal valve IGT Br 923. Saku, Oandu Stage. A gerontic specimen showing adductor scars. Interior and exterior views. × 2.

Figs. 7, 9. *Vellamo oandoensis* Öpik, 1934. Dorsal valve IGT Br 508. Rakvere, Oandu Stage. Interior and exterior views. × 2.

Figs. 10, 11, 13. *Vellamo parva* Öpik, 1930. Complete shell TUG 56/26. Harku, Kukruse Stage. Exterior, anterior, and lateral views. × 2.

Figs. 12, 14. *Vellamo parva* Öpik, 1930. Dorsal valve IGT Br 516. Figured by Öpik (1934, pl. 11, figs. 1a,b) as *V. rara* Öpik. Interior and exterior views. × 2.

PLATE V

Fig. 1. *Vellamo silurica* Öpik, 1934. Dorsal valve IGT Br 500. Porkuni, Porkuni Stage. Interior view. × 2.

Figs. 2, 3. *Vellamo* cf. *phrygia* Öpik, 1934. Ventral valve TUG 77/15. Oandu, Keila Stage. Lateral and exterior views. × 2.

Figs. 4, 5. *Vellamo defecta* Öpik, 1934. Holotype. Dorsal valve IGT Br 501. Vasalemma, Oandu Stage. Interior and exterior views. × 2.

Figs. 6–8, 10. *Vellamo phrygia* Öpik, 1934. Holotype. Ventral valve IGT Br 486. Saue, Keila Stage. Posterior, exterior, anterior, and lateral views. × 2.

Figs. 9, 11, 13, 14. *Vellamo silurica* Öpik, 1934. Holotype. Ventral valve IGT Br 499. Porkuni, Porkuni Stage. Exterior, lateral, interior, and posterior views. × 1.5.

Figs. 12, 15. *Vellamo symmetrica* Öpik, 1934. Holotype. Ventral valve IGT Br 484. Paluküla, Vormsi Stage. Posterior and exterior views. × 1.5.

PLATE VI

Figs. 1–3, 6. *Vellamo aenigma* Öpik, 1934. Ventral valve TUG 892/1. Vaardi, Pirgu Stage. Exterior, lateral, posterior, and interior views. Natural size.

Figs. 4, 5. *Vellamo magna* Öpik, 1934. Dorsal valve TUG 72/60. Rakvere, Keila Stage. Exterior and interior views. Natural size.

Figs. 7–10. *Vellamo magna* Öpik, 1934. Holotype. Ventral valve IGT Br 496. Rakvere, Keila Stage. Posterior, exterior, lateral, and anterior views. × 1.2.

Fig. 11. *Vellamo wesenbergiensis* (Pahlen, 1877). Dorsal valve IGT Br 487. Rägavere, Rakvere Stage. Figured by Öpik (1934, pl. 10, fig. 7) as *Vellamo wesenbergensis auriculata* Öpik. Interior view. Showing strong radial ridges on the interior of the adductor scars. × 1.2.

Figs. 13, 15. *Vellamo wesenbergiensis* (Pahlen, 1877). Dorsal valve IGT Br 493. Rägavere, Rakvere Stage. Showing unusual pattern of adductor scars consisting of radial and transverse ridges. × 1.2.

Figs. 12, 14, 16–18. *Vellamo wesenbergiensis* (Pahlen, 1877). Neotype. Complete shell IGT Br 494. Rägavere, Rakvere Stage. × 1.2.

Alikhova (1953) described a new species, *Vellamo praeemarginata.* She explained remarkable variability and asymmetry of *V. wesenbergensis* with ecological reasons. Nasedkina (1970) mentioned numerous *Vellamo* species from the western slope of the North and Middle Urals, among them three new species and one new subspecies. Species of *Vellamo* were also described by Bondarev (1968) and Oradovskaya (1977).

Vellamo species from the British Isles have been reviewed and described by Williams (1963), Wright (1964), Mitchell (1977), Cocks (1978), Hiller (1980), and Harper (1989). American species have been described by Raymond (1921), Twenhofel (1927), Wilson (1946), and Bolton (1961). Rare specimens have been reported from Algeria (Termier & Termier, 1950), Belgium (Sheehan, 1987), and Tasmania (Laurie, 1991).

SYSTEMATIC DESCRIPTIONS

Superfamily CLITAMBONITOIDEA Winchell & Schuchert, 1893

Family CLITAMBONITIDAE Winchell & Schuchert, 1893

Genus *Vellamo* Öpik, 1930, emend.

1930a *Clitambonites* (*Vellamo*) n. subg.; Öpik, p. 212.
1932 *Vellamo* Öpik; Shuchert & Cooper, p. 114.
1934 *Vellamo* Öpik; Öpik, p. 98.
1953 *Vellamo* Öpik; Alikhova, p. 78.
1955 *Vellamo* Öpik; Schimer & Schrock, p. 297.
1965 *Vellamo* Öpik; Williams & Wright, p. H352.
1970 *Vellamo* Öpik; Nasedkina, p. 43.
1973 *Vellamo* Öpik; Nasedkina, p. 124.

Type species. *Orthis verneuilii* Eichwald, 1841; p. 5, pl. 2, figs. 3–5.

Diagnosis. Shell up to 32 mm wide and up to 40 mm long, planoconvex to ventribiconvex. Outline transversely semiovate to semicircular, subquadrate or blazon-like. Maximum width at hinge line or anterior to hinge line. Anterior margin rounded to emarginate (B-shaped), anterior commissure slightly sulcate or rectimarginate. Ornamentation costellate, ribs mostly of equal size. Concentric growth lines occasionally visible, imbrication developed at the anterior part of the ventral valve, or rarely, all over the exterior surface.

Ventral valve often asymmetrical, either due to distorted growth or twisted apex. Ventral interarea up to 25 mm high, catacline to apsacline, rarely procline with flat, concave or irregularly terraced profile. Delthyrium about one-third as wide as hinge line, closed by convex deltidium. Deltidium perforated by large foramen, sealed during lifetime in some species.

Dorsal valve flat or slightly convex. Dorsal interarea short, anacline, notothyrium closed by well-developed chilidium. Notothyrial cavity divided by simple ridge-like cardinal process. Dorsal adductor field quadripartite with the anterior and posterior pairs separated by a clearly defined ridge perpendicular to the median ridge. Commonly the scars are of equal size or the anterior pair is smaller than the posterior pair. Some species show poorly defined adductor fields.

Shell substance impunctate.

Discussion. Bondarev (1968, p. 71) diagnosed *Vellamo* (?) *summa* as a species with pseudopunctate shell substance. His description of pseudopunctation that "can be recognized on the outer layer of the shell near the anterolateral margin, where on the surface of the ribs small circular holes are radially disposed" is a perfect diagnosis for aditicules, a type of exopunctae that accommodated setal bristles and are a part of the sensory system of brachiopods (Wright, 1981). In fact, aditicules are passing through the entire shell, but can normally be seen only near the shell margin as they get sealed inside the shell and are therefore visible only at the outer surface of the shell. Wright & Rubel (1996) figured several species of *Kullervo* Öpik, 1932, possessing aditicules, and mentioned their absence as a generic character in *Apomatella* Schuchert & Cooper, 1931. The present study does not attribute a diagnostic value to the absence or presence of aditicules, due to their sporadic occurrence. They are better preserved and exposed in specimens showing imbricative sculpture at the anterolateral part of the shell.

Species assigned apart from the species described below:

Vellamo diconvexa Nasedkina, 1970 (Nasedkina, pp. 46–47, figs. 5–7; pl. 9, fig. 7).
Orthisina diversa Shaler, 1865 (Shaler, p. 67).
Skenidium Grayiae Davidson, 1883 (Davidson, p. 175, pl. 11, figs. 3–9).
Vellamo mitra Nasedkina, 1970 (Nasedkina, pp. 49–50, pl. 9, figs. 1–4).
Vellamo praeemarginata grandis Nasedkina, 1970 (Nasedkina, pp. 44–45, pl. 8, figs. 1–4).
Vellamo putukuneiensis Oradovskaya, 1977 (Oradovskaya, pp. 91–93, pl. 3, figs. 5–7).
Skenidium? *Shallockiense* Davidson, 1883 (Davidson, p. 174, pl. 11, figs. 6, 7.)
Vellamo sinclairi Wilson, 1946 (Wilson, p. 115, pl. 3, fig. 30).
Vellamo sulculata Wright, 1964 (Wright, pp. 236–240, pl. 10, figs. 1, 2, 4, 5, 8, 9, 11, 12, 14).
Vellamo (?) *summa* Bondarev, 1968 (Bondarev, p. 71; pl. 4, figs. 9–13; pl. 5, figs. 1–4).
Clitambonites trentonensis Raymond, 1921 (Raymond, p. 27, pl. 7, figs. 6, 7).
Vellamo typylica Nasedkina, 1970 (Nasedkina, pp. 47–49, pl. 8, figs. 8, 9).
Vellamo sp. (Laurie, 1991, p. 49, fig. 35c).
Vellamo sp. (Mitchell, 1977, p. 65, pl. 11, figs. 17, 18).
Vellamo sp. (Sheehan, 1987, p. 28, pl. 7, figs. 21–23).
Vellamo sp. (Termier & Termier, 1950, p. 18, pl. 2, figs. 4–6).
Vellamo sp. (Williams, 1963, p. 428, pl. 10, figs. 14, 18).
Vellamo sp. (Wright, 1964, p. 241, pl. 10, figs. 6, 7).

Species rejected. *Vellamo chinensis* (Weller).

The specimen figured as *Vellamo chinensis* (Weller) (Fu, 1982) is well preserved, small, with fine costellate ornamentation, convex ventral and slightly convex dorsal valve. All the studied *Vellamo* species have a big deltidium, about 1/3 of the length of the hinge line, but the deltidium of the figured specimen is considerably smaller. The figured specimen lacks foramen and belongs more likely to the genus *Eremotoechia* Cooper, 1956.

Occurrence. Middle and Upper Ordovician. Belgium, British Isles, East Baltic and Podolia, western slope of the Ural Mountains and the Vaigach Island, Northeast Asia, eastern North America, Tasmania, Algeria.

Vellamo verneuilii (Eichwald, 1841)

Plate I, figures 1–13

1841 *Orthis verneuilii* Eichwald, p. 51, pl. 2, figs. 3–5.
1845 *Orthis verneuilii* Eichwald; Murchison et al., vol. 2, p. 201, pl. 11, fig. 8; pl. 12, fig. 1.
1877 *Orthisina verneuilii* Eichwald; Pahlen, p. 35, pl. 4, figs. 4–6, 11–15.
1930b *Clitambonites* (*Vellamo*) *verneuili* (Eichwald); Öpik, p. 212.
1934 *Vellamo verneuili* (Eichwald); Öpik, p. 100, pl. 13, figs. 1, 4; pl. 14, figs. 1–7b.
1934 *Vellamo sauramoi* n. sp.; Öpik, pl. 13, figs. 8, 8a,b.
1976 *Vellamo verneuili* (Eichwald); Tsegelnyuk, pp. 44–46, pl. 5, fig. 14; pl. 6, fig. 1.
non 1973 *Vellamo* cf. *verneuili* (Eichwald); Nasedkina, pp. 125–126, pl. 22, figs. 9–12.

Neotype. Ventral valve IGT Br 477; Vormsi Stage, Kõrgessaare, Estonia. Pl. I, figs. 1, 2, 5.

Material. 140 ventral valves, 61 dorsal valves, 64 complete shells.

Diagnosis. Shell up to 32 mm long and up to 35 mm wide; semiovate, semicircular, or subquadrate. Maximum width of the shell at hinge line to slightly anterior to midlength, cardinal extremities acute to obtuse, sides concave to straight, anterior margin straight to bulging, anterior commissure rectimarginate. Number of ribs 6–9 in 5 mm at 5 mm from ventral beak, 5–7 at the anterolateral margin. Lateral profile of the ventral valve convex, the highest point at apex to at midlength. Ventral interarea up to 17 mm high, planar to concave, apsacline to orthocline. Foramen subapical, sealed. *Spondylium simplex* supported by ridge extending to anterior margin. Dorsal valve flat to slightly concave, without sulcus or with weak sulcus.

Discussion. Öpik (1934) described a single medium-size specimen from Vormsi, Vormsi Stage, as *V. sauramoi*. The specimen shows subquadrate outline, a nearly straight anterior margin, straight sides, and flat lateral profile. Its foramen is sealed and the ornamentation is coarse. Obviously the specimen described as *V. sauramoi* is a juvenile specimen of *V. verneuilii*.

Occurrence. Nabala, Vormsi, and Pirgu stages. Haapsalu, Kõrgessaare, Moe, Paluküla, Paopää, Saxby, Tapa, Torma, Uuemõisa, and Voore outcrops. Ingria (Alikhova, 1953).

Vellamo leigeri Öpik, 1934

Plate I, figures 14–16

1934 *Vellamo leigeri* n. sp.; Öpik, pp. 105–106, pl. 12, figs. 5–5c.

Holotype. Dorsal and ventral valves IGT Br 483; Vormsi Stage, Paluküla, Estonia.

Remarks. *V. leigeri* occurs in the Vormsi Stage together with *V. verneuilii*. It differs from the latter in finer ornamentation. Specimens of *V. verneuilii* with a width of 20 mm show a sealed foramen. The single specimen of *V. leigeri* possesses open foramen and thin shell, not common in *V. verneuilii*.

Vellamo praeemarginata Alichova, 1953

Plate II, figures 1, 2, 4, 5

1953 *Vellamo praeemarginata* n. sp.; Alikhova, pp. 79–80, pl. 10, fig. 12.

Holotype. Ventral valve from the Idavere Stage, St Petersburg region. Kept in the private collection of Alikhova.

Material. 19 ventral valves, 4 dorsal valves.

Diagnosis. Shell up to 15 mm long and up to 22 mm wide, semiovate to subquadrate. Maximum width of the shell at hinge line to slightly anterior to midlength, cardinal extremities acute, sides concave, anterior margin emarginate, anterior commissure rectimarginate to sulcate. Number of ribs 9–12 in 5 mm at 5 mm from ventral beak, 7–8 at the anterolateral margin. Ventral interarea up to 8 mm high, planar to concave, catacline to apsacline. Dorsal valve flat, with median sulcus.

Discussion. *V. praeemarginata* is a close species to *V. pyramidalis*. It differs from the latter in a slightly bigger shell and finer ornamentation.

Occurrence. Haljala Stage. Idavere and Aluvere outcrops. Ingria (Alikhova, 1953).

Vellamo ambisulcata Öpik, 1934

Plate II, figures 3, 6, 8, 9, 11, 12, 14

1934 *Vellamo ambisulcata* n. sp.; Öpik, p. 112, pl. 12, figs. 9a–c.

Holotype. Conjoined valves IGT Br 502; Keila Stage, Rakvere, northern Estonia.

Material. 4 complete shells, 10 ventral valves, 9 dorsal valves.

Diagnosis. Shell up to 15 mm long and up to 21 mm wide, semiovate to subquadrate. Maximum width of the shell at hinge line, cardinal extremities acute, sides concave, anterior margin emarginate, anterior commissure rectimarginate to sulcate. Number of ribs 8–9 in 5 mm at 5 mm from ventral beak, 5–8 at the anterolateral margin. Lateral profile of the ventral valve plain to convex, the highest point at apex. Ventral interarea up to 9 mm high, planar to concave, catacline to apsacline. Dorsal valve flat to slightly convex, without sulcus or with weak sulcus. Notothyrial platform lying anterior to dorsal interarea.

Discussion. *V. ambisulcata* is one of the four species of *Vellamo* found in the Keila Stage. *V. ambisulcata* resembles *V. emarginata* in having acute cardinal angles, concave sides, and emarginate anterior margin, differing in the interior morphology of the dorsal valve. The notothyrial platform which in most species of *Vellamo* lies almost flush with the hinge line has been dispositioned anteriorly to the hinge line in this species. *V. ambisulcata* shows coarser ribbing than *V. emarginata*.

Occurrence. Keila Stage. Jälgimäe, Oandu, Rakvere, and Saku outcrops. Core sections: Kuusiku – 15.75–15.80 m; Saku – 13.42–13.47 m; Tuula – 11.2 m, and Voore – 16.05 m.

Vellamo emarginata (Pahlen, 1877)

Plate II, figures 7, 10, 13, 15–18

1877 *Orthisina emarginata* n. sp.; Pahlen, p. 38, pl. 4, figs. 16–18.
1934 *Vellamo emarginata* (Pahlen); Öpik, pp. 110–111, pl. 12, figs. 4–6.
1953 *Vellamo emarginata* (Pahlen); Alikhova, pp. 80–82, pl. 10, figs. 1–3.

Type. Pahlen (1877) did not select the holotype. His collections were partly destroyed during World War II, partly distributed to several schools in Estonia after the war. The part housed in the Museum of the Natural History in Tallinn does not contain any specimens belonging to the genus *Vellamo*. The specimen kept in the museum under the number 1201 G1:404 resembles *V. emarginata* figured on the drawing by Pahlen (1877, pl. 4, figs. 16–18) but its origin and locality are unknown.

Neotype. Complete shell TUG 72/148; Keila Stage, Oandu, Estonia.

Material. 20 complete shells, 24 ventral valves, 7 dorsal valves.

Diagnosis. Shell up to 22 mm long and up to 28 mm wide, semiovate to subquadrate. Maximum width of the shell at hinge line or slightly anterior to midlength, cardinal extremities acute, sides concave, anterior margin emarginate, anterior commissure rectimarginate to sulcate. Number of ribs 10–11 in 5 mm at 5 mm from ventral beak, 10–11 at the anterolateral margin. Lateral profile of the ventral valve plain to convex, the highest point at apex to slightly anterior to apex. Ventral interarea up to 12 mm high, planar to concave, apsacline. Dorsal valve flat to slightly convex, without sulcus or with weak sulcus. Notothyrial platform lying anterior to hinge line.

Discussion. *V. emarginata* resembles *V. ambisulcata*. *V. emarginata* is bigger, shows finer ornamentation than *V. ambisulcata* and the maximum width of the adult shell is slightly anterior to midlength.

Occurrence. Haljala and Keila stages. Allika, Aluvere, Aru, Kurtna, Oandu, Pääsküla, Rakvere, Saku, Sompa, and Sõmeru outcrops.

Vellamo pyramidalis (Pahlen, 1877)

Plate III, figures 1–11, 13

1877 *Orthisina pyramidalis* n. sp.; Pahlen, p. 39, pl. 4, figs. 19–21.
1930a *Clitambonites* (*Vellamo*) *pyramidalis* (Pahlen); Öpik, p. 213, pl. 19, figs. 220–222, 225, 226.
1930a *Clitambonites* (*Vellamo*) *pyramidalis arcuatus* n. subsp.; Öpik, p. 215, pl. 19, fig. 223.
1930a *Clitambonites* (*Vellamo*) *pyramidalis pahleni* n. subsp.; Öpik, p. 216, pl. 19, fig. 224.
1930a *Clitambonites* (*Vellamo*) *pyramidalis simplex* n. subsp.; Öpik, p. 217, pl. 19, figs. 219, 227.
1930b *Clitambonites* (*Vellamo*) *viruanus* n. sp.; Öpik, p. 15–16, pl. 2, figs. 14a–c.
1934 *Vellamo simplex* A. Ö.; Öpik, p. 115, pl. 11, figs. 3a,b.
1934 *Vellamo pyramidalis* (Pahlen); Öpik, p. 115, pl. 11, figs. 4, 5.

Neotype. Ventral valve TUG 39/76; Kukruse Stage, Kohtla, Estonia.

Material. 11 complete shells, 67 ventral valves, 26 dorsal valves.

Diagnosis. Shell up to 9 mm long and up to 16 mm wide, semiovate to subquadrate. Maximum width of the shell at hinge line, cardinal extremities acute, sides concave to straight, anterior margin emarginate to rounded, anterior commissure rectimarginate to sulcate. Number of ribs 7–10 in 5 mm at 5 mm from ventral beak, 6–10 at the anterolateral margin. Ventral interarea up to 8 mm high, planar to concave, catacline to apsacline. Dorsal valve flat, with median sulcus. Anterior pair of adductor scars larger than posterior pair or equal to posterior pair.

Discussion. Öpik (1930a, 1934) described *V. pyramidalis* as being distinct from *V. simplex*, also two subspecies were described. The present study regards them as

intraspecific varieties. *V. pyramidalis pahleni* and *V. pyramidalis arcuatus* should be treated as juvenile specimens. *V. simplex* does not show remarkable differences from *V. pyramidalis*. *V. pyramidalis* occurs in the same stages with *V. parva*. It is distinguished from the latter by coarser ornamentation, smaller shell, and acute cardinal angles.

Occurrence. Lasnamägi, Uhaku, Kukruse, and Haljala stages. Allika, Harku, Kohtla, Kostivere, Küttejõud, Lasnamägi, Purtse, and Uhaku outcrops.

Vellamo anijana Öpik, 1934

Plate III, figures 12, 14–16

1934 *Vellamo anijana* n. sp.; Öpik, pp. 114–115, pl. 12, fig. 10.

Holotype. Complete shell IGT Br 510; Haljala Stage, Anija, northern Estonia.

Material. 2 complete shells, 7 ventral valves, 1 dorsal valve.

Diagnosis. Shell up to 16 mm long and up to 19 mm wide, semiovate to subquadrate. Maximum width of the shell at hinge line, cardinal extremities acute, sides concave, anterior margin emarginate to straight, anterior commissure sulcate. Number of ribs 5–7 in 5 mm at 5 mm from ventral beak, 7–8 at the anterolateral margin. Lateral profile of the ventral valve convex, the highest point at apex to slightly anterior to apex. Ventral interarea up to 8 mm high, planar to concave, catacline to apsacline. Dorsal valve flat, with weak sulcus.

Discussion. *V. anijana* occurs in the Haljala Stage together with *V. praeemarginata* and *V. emarginata,* differing in coarser ornamentation. In shape and outline similar to adult *V. pyramidalis*, but the ventral valve of *V. anijana* is more convex with the highest point of the valve anterior to the apex.

Occurrence. Haljala Stage. Allika, Anija, Harku, Sõjamägi, and Soonurme outcrops.

Vellamo oandoensis Öpik, 1934

Plate IV, figures 1–9

1934 *Vellamo oandoensis* n. sp.; Öpik, pp. 113–114, pl. 12, figs. 11a–14.

Holotype. Complete shell IGT Br 505; Oandu Stage, Rakvere, northern Estonia.

Material. 15 complete shells, 68 ventral valves, 35 dorsal valves.

Diagnosis. Shell up to 17 mm long and up to 27 mm wide, subquadrate. Maximum width of the shell at hinge line to slightly anterior to midlength, cardinal extremities right-angled to obtuse, sides straight, anterior margin emarginate to straight. Number of ribs 8–9 in 5 mm at 5 mm from ventral beak, 8–11 at the anterolateral margin. Lateral profile of the ventral valve plain to convex, the

highest point at apex. Ventral interarea up to 13 mm high, planar, procline to apsacline. Dorsal valve flat to slightly convex, with median sulcus. Dorsal adductor field obscure.

Discussion. *V. oandoensis* differs from other species of the Keila and Oandu stages in subquadrate outline, straight sides, and thin shell. The dorsal adductor field is usually poorly defined, only gerontic specimens show typical adductor scars.

Occurrence. Keila and Oandu stages. Rakvere, Oandu, Jälgimäe, Tõrremäe, Saku, and Vasalemma outcrops. Core sections: Vasalemma – 3.15 m; Kaasiku – 16.95 m.

Vellamo parva Öpik, 1930

Plate IV, figures 10–14

1930a *Clitambonites* (*Vellamo*) *parvus* n. sp.; Öpik, p. 219, pl. 21, fig. 279.
1930a *Clitambonites* (*Vellamo*) *ultimus* n. sp.; Öpik, p. 219, pl. 22, fig. 280.
1934 *Vellamo parva* A. Öpik; Öpik, p. 116, pl. 11, figs. 2a,b.
1934 *Vellamo rara* n. sp.; Öpik, p. 116, pl. 2, figs. 5a,b; pl. 11, figs. 1a,b.

Holotype. Dorsal valve IGT Br 300 (No. 279); Keila Stage, Kohtla, Estonia.

Material. 8 complete shells, 17 ventral valves, 9 dorsal valves.

Diagnosis. Shell up to 23 mm long and up to 21 mm wide, semiovate to subquadrate. Maximum width of the shell at hinge line to slightly anterior to midlength, cardinal extremities right-angled to obtuse, sides straight, anterior margin straight to rounded, anterior commissure rectimarginate. Number of ribs 9–15 in 5 mm at 5 mm from ventral beak, 14–17 at the anterolateral margin. Lateral profile of the ventral valve convex, the highest point at apex to slightly anterior to apex. Ventral interarea up to 9 mm high, planar to concave, catacline to apsacline. Dorsal valve slightly convex, without sulcus or with weak sulcus. Dorsal adductor field obscure.

Discussion. Öpik (1930a, 1934) described three different species – *V. ultimus, V. parva*, and *V. rara*. The present study regards them in the limits of intraspecific variability. *V. parva*, figured by Öpik in 1930a (pl. 21, fig. 279), is a juvenile specimen. The dorsal valves of *V. rara* (figured by Öpik, 1934; pl. 11, figs. 1a,b) and *V. ultimus* (figured by Öpik, 1930a; pl. 22, fig. 280) show similar internal and external features. Deciding by the acute cardinal angles, the specimen figured as *V. ultimus* is slightly younger than the specimen figured as *V. rara.* Also *V. ultimus* Öpik shows slight sulcus on the dorsal valve, but the dorsal valve of *V. rara* Öpik is flat. The outline of both specimens is subquadrate, the ornamentation is fine and the adductor field is oblique. These are also the main characters distinguishing *V. parva* from *V. pyramidalis*, as they both occur in the same stages.

Occurrence. Lasnamägi, Uhaku, Kukruse, and Haljala stages. Kohtla, Allika, Harku, Humala, Sõjamägi, Lasnamägi, and Kostivere outcrops.

Vellamo silurica Öpik, 1934

Plate V, figures 1, 9, 11, 13, 14

1934 *Vellamo silurica* n. sp.; Öpik, p. 111, pl. 12, figs. 1a,b, 2.

Holotype. Ventral valve IGT Br 499; Porkuni Stage, Porkuni, Estonia.

Remarks. The shape and size of the ventral valve of *V. silurica* are similar to those of *V. symmetrica*. The main difference lies in the ornamentation. *V. silurica* shows coarser ornamentation than *V. symmetrica*.

Vellamo defecta Öpik, 1934

Plate V, figures 4, 5

1934 *Vellamo defecta* n. sp.; Öpik, pp. 111–112, pl. 12, figs. 3a,b.

Holotype. Dorsal valve IGT Br 501; Oandu Stage, Vasalemma, northern Estonia.

Remarks. *V. defecta* occurs in the Oandu Stage together with *V. oandoensis*. It differs from the latter in the semiovate shell shape, acute cardinal extermities, and concave sides. It is the only species in the genus without cardinal process.

Vellamo phrygia Öpik, 1934

Plate V, figures 2, 3, 6–8, 10

1934 *Vellamo phrygia* n. sp.; Öpik, p. 107, pl. 12, figs. 6, 7.

Holotype. Ventral valve IGT Br. 486; Keila Stage, Saue, Estonia.

Material. 4 ventral valves.

Diagnosis. Shell up to 18 mm long, 24 mm wide, semiovate to semicircular. Maximum width of the shell at hinge line to slightly anterior to hinge line, cardinal extremities acute to obtuse, anterior margin rounded, anterior commissure rectimarginate. Number of ribs 7–8 in 5 mm at 5 mm from ventral beak, 8–10 at the anterolateral margin. Imbrication developed all over the surface. Lateral profile of the ventral valve plain, the highest point at apex. Ventral interarea up to 25 mm high, planar to concave, catacline.

Discussion. *V. phrygia* differs greatly from other *Vellamo* species in its high ventral valve, semicircular outline and typical imbricative sculpture. A specimen of *V.* cf. *phrygia* (Pl. V, fig. 3) shows an apsacline, high ventral valve, but lacks imbrication. However, the growth lines are uncommonly strong.

Occurrence. Keila Stage. Saue and Oandu outcrops. Padise core – 11.0 m.

Vellamo symmetrica Öpik, 1934

Plate V, figures 12, 15

1934 *Vellamo symmetrica* n. sp.; Öpik, p. 106, pl. 13, figs. 2, 3.

Holotype. Ventral valve IGT Br 484; Vormsi Stage, Paluküla, Estonia.

Remarks. *V. symmetrica* occurs in the Vormsi Stage together with *V. leigeri* and *V. verneuilii.* It differs from them in subquadrate outline and absence of imbrication.

Vellamo aenigma Öpik, 1934

Plate VI, figures 1–3, 6

1934 *Vellamo aenigma* n. sp.; Öpik, p. 117, pl. 19, figs. 8a–c.

Holotype. Silicified ventral valve IGT Br 518; Porkuni, Estonia. A redeposited specimen from Quaternary till. Nabala, Vormsi or Pirgu stages.

Material. 4 complete shells; 5 ventral valves, 2 of them partly silicified; one silicified fragment of ventral valve; 5 dorsal valves.

Diagnosis. Shell up to 30 mm long and up to 40 mm wide, semiovate to semicircular. Maximum width of the shell at hinge line or slightly anterior to hinge line. Cardinal extremities acute, sides straight, anterior margin rounded, anterior commissure rectimarginate. Number of ribs 9–10 in 5 mm at 5 mm from ventral beak, 6–9 at the anterolateral margin. Lateral profile of the ventral valve plain, with the highest point at apex. Ventral interarea up to 13 mm high, planar, apsacline. Foramen apical, sealed. Dorsal valve flat, without sulcus.

Discussion. *V. aenigma* occurs in the Pirgu Stage together with *V. verneuilii* and differs from it in flat ventral valve and fine ornamentation. From other species of *Vellamo* it differs in the high, apical position of small foramen, about 1–2 mm in diameter.

Occurrence. Vardi and Ümeru outcrops. Lower part of the Pirgu Stage. The material described by Öpik (1934) was collected from till at Porkuni and its original stratigraphical position is not clear.

Vellamo magna Öpik, 1934

Plate VI, figures 4, 5, 7–10

1934 *Vellamo magna* n. sp.; Öpik, pp. 109–110, pl. 12, figs. 7, 8.

Holotype. Ventral valve IGT Br 496; Keila Stage, Rakvere, northern Estonia.

Material. 6 complete shells, 29 ventral valves, 12 dorsal valves.

Diagnosis. Shell up to 30 mm long and up to 37 mm wide; semiovate, semicircular, or subquadrate. Maximum width of the shell at hinge line to at midlength, cardinal

extremities acute to obtuse, sides straight, anterior margin emarginate to rounded, anterior commissure rectimarginate to sulcate. Number of ribs 9–10 in 5 mm at 5 mm from ventral beak, 8–9 at the anterolateral margin. Lateral profile of the ventral valve plain to convex, the highest point at apex to slightly anterior to apex. Ventral interarea up to 17 mm high. *Spondylium simplex* supported by ridge extending to anterior margin. Dorsal valve flat, without sulcus or with weak sulcus.

Discussion. *V. magna* occurs in the Keila Stage together with *V. emarginata*, *V. ambisulcata*, *V. phrygia*, and *V. oandoensis*. An adult specimen of *V. magna* is easily distinguishable from those by larger size, subquadrate shell shape, and straight sides. The dorsal valve of a preadult specimen resembles that of *V. wesenbergiensis*. The main difference is the finer ornamentation of *V. magna*.

Occurrence. Keila Stage. Jälgimäe, Kehra, Oandu, Rakvere, Saku, Saue, Sõmeru, and Tuula outcrops. Saku core – 11.1–11.4 m.

Vellamo wesenbergiensis (Pahlen, 1877)

Plate VI, figures 11–18

1877 *Orthisina verneuilii wesenbergiensis* Pahlen, p. 35, pl. 4, figs. 7–10.
1934 *Vellamo wesenbergensis* (Pahlen); Öpik, p. 108, pl. 10, figs. 2–5, 8–10; pl. 30, fig. 2.
1934 *Vellamo wesenbergensis auriculata* Öpik; Öpik, p. 109, pl. 10, figs. 6a,b, 7.
1953 *Vellamo wesenbergensis* (Pahlen); Alikhova, p. 82, pl. 11, figs. 1–8.
non 1973 *Vellamo wesenbergensis* (Pahlen); Nasedkina, p. 124, pl. 22, figs. 4, 8.

Neotype. Complete shell IGT Br 494; Rakvere Stage, Rägavere, Estonia.

Material. 14 complete shells, 9 ventral valves, 13 dorsal valves.

Diagnosis. Shell up to 30 mm long and up to 37 mm wide, semiovate. Maximum width of the shell at hinge line to at midlength, cardinal extremities acute to obtuse, sides concave to straight, anterior margin emarginate to rounded, anterior commissure rectimarginate to sulcate. Number of ribs 5–7 in 5 mm at 5 mm from ventral beak, 6–8 at the anterolateral margin. Lateral profile of the ventral valve plain to convex, the highest point at apex to slightly anterior to apex. Ventral interarea up to 13 mm high, planar to concave, apsacline. Dorsal valve flat to slightly concave, without sulcus or with weak sulcus.

Discussion. *V. wesenbergiensis* is closely similar to *V. verneuilii*, differing in open foramen of adult specimens and slightly coarser ornamentation. The outline is typically semiovate, never shows bulging anterior margin as in *V. verneuilii*. *V. wesenbergiensis* is the only species in the Rakvere Stage.

Nasedkina (1973) described 57 specimens from the Rassocha Stage (Ashgill), the Rassocha River, western slope of the North Urals as *Vellamo wesenbergiensis*. The described species differs from the Estonian species in having a convex dorsal valve and ornamentation about twice as fine (10–12 ribs

per 5 mm) as in the Estonian species. Obviously the described specimens belong to a different species.

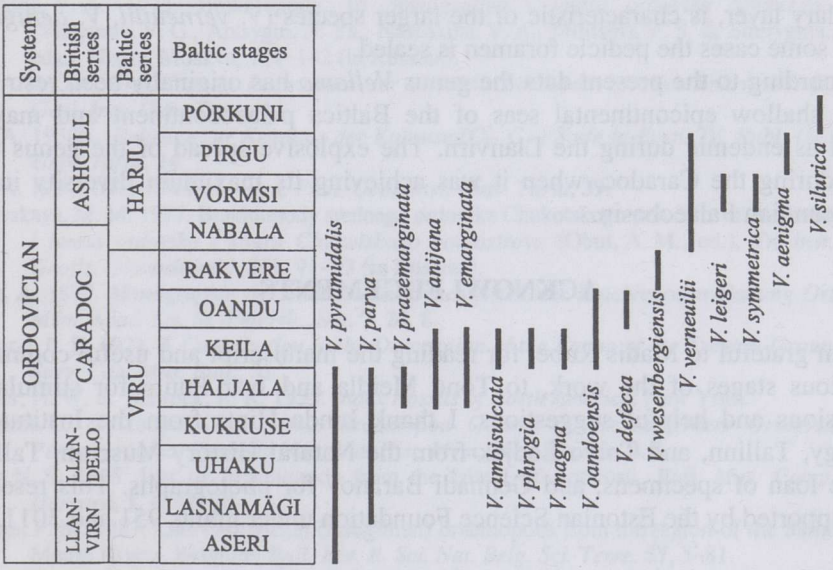
Occurrence. Rakvere Stage. Rägavere and Rakvere outcrops. Ingria (Alikhova, 1953).

DEVELOPMENT OF THE GENUS *VELLAMO* IN ESTONIA

Vellamo is a widely spread clitambonitidine genus in the middle–upper Ordovician. Of 34 species assigned, 16 have been described from Estonia and Ingria (St Petersburg region). Their distribution of the species is summarized in Table 2. Three distinct stages can be noted in the development of the genus: early Viru, mid-Viru, and late Viru/Harju.

Table 2

Stratigraphical distribution of Estonian *Vellamo* species



The earliest known *Vellamo* species is *V. pyramidalis*, which appeared in the Aseri time. *V. parva* appeared in the Lasnamägi Stage. Both species are small to medium-sized and characterized by thin shells. They are the only representatives of the genus during the early Viru epoch, the Kukruse time inclusive.

The mid-Viru development stage began with the appearance of three new species – *V. anijana*, *V. praeemarginata*, and *V. emarginata* – in the Haljala time. The Keila time marked the highest diversity for the genus *Vellamo*; four new species were added to the record: *V. ambisulcata*, *V. phrygia*, *V. magna*, and *V. oandoensis*. All nine species which existed during the Keila time show indisputably different sets of characters and should be regarded as valid taxa. The

Vellamo species of medium size prevailed during the Keila time, but some species with a thick shell and anteriorly arranged notothyrial platform are recorded as well (*V. magna*, *V. ambisulcata*). Of the nine Keila species, only *V. oandoensis* continued its existence during the Oandu time. A remarkable diversity fall co-occurs with the Keila/Oandu boundary event which is well documented in the Estonian succession (Hints et al., 1989).

The post-Keila epoch shows mostly successive taxa. Apart from *V. oandoensis*, the single specimen of *V. defecta* is documented from the Oandu Stage. In the Rakvere Stage, only *V. wesenbergiensis* has been recorded. In the Nabala Stage it was replaced by *V. verneuilii*, the type species of the genus. This species is the most common *Vellamo* species in the Harju Series, ranging into the Porkuni Stage. The Vormsi time marks the appearance of *V. leigeri* and *V. symmetrica*, rare short-ranged taxa with very distinct sets of morphological characters. The rare species, *V. aenigma* of the Pirgu time and *V. silurica* of the Porkuni time complement the record of *Vellamo* in the Ordovician of Estonia. Within the species of the Harju epoch, medium-sized species are common while the maximum size of the species gradually increases at the end of the Ordovician. A heavy shell, with a thick secondary layer, is characteristic of the larger species (*V. verneuilii*, *V. aenigma*), and in some cases the pedicle foramen is sealed.

According to the present data the genus *Vellamo* has originally been restricted to the shallow epicontinental seas of the Baltica palaeocontinent and may be treated as endemic during the Llanvirn. The explosive spread of the genus took place during the Caradoc, when it was achieving its maximum diversity in the Baltoscandian Palaeobasin.

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REFERENCES

Alikhova, T. N. 1953. *Rukovodyashchaya fauna brakhiopod ordovikskikh otlozhenij severo-zapadnoj chasti Russkoj platformy*. Gosudarstvennoe Izdatel'stvo Geologicheskoj Literatury, Moskva (in Russian).

Bolton, T. E. 1961. Ordovician and Silurian formations of Anticosti Island, Quebec. *Bull. Geol. Surv. Can.*, **61**, 26, 1–18.

Bondarev, V. G. 1968. Stratigrafiya i kharakternye brakhiopody ordovikskikh otlozhenij yuga Novoj Zemli, o. Vaigach i severnogo Paj-Khoya. *Trudy NIIGA*, **157**, 3–144 (in Russian).

Cocks, L. R. M. 1978. *A Review of British Lower Palaeozoic Brachiopods, Including a Synoptic Revision of Davidson's Monograph. Palaeontogr. Soc. Monogr. Lond.*, **131**, 549.

Davidson, T. 1883. *Monograph of the British Fossil Brachiopoda. Silurian Supplement*. Vol. 5, Pt. 2., Palaeontogr. Soc., London.

Eichwald, E. 1841. *Die Uhrwelt Russlands durch Abbildungen erlaeutert.* St. Petersburg.
Fu, Li-Pu. 1982. *Palaeontological Atlas of Northwest China. Precambrian and Early Paleozoic, Shaanxi-Gansu-Ningxia, Vol. 1.* Geological Publishing House, Beijing, China.
Harper, D. A. T. 1989. *Brachiopods from the Upper Ardmillian Succession (Ordovician) of the Girvan District, Scotland, Part 2. Palaeontogr. Soc. Monogr. Lond.*, **142**, 579, 79–128.
Hiller, N. 1980. Ashgill Brachiopoda from Gill Ceiriog District, North Wales. *British Mus. (Nat. Hist.), Geol. Ser.*, **34**, 3, 109–216.
Hints, L., Meidla, T., Nõlvak, J. & Sarv, L. 1989. Some specific features of the Late Ordovician evolution in the Baltic basin. *Proc. Acad. Sci. ESSR. Geol.*, **38**, 2, 83–87.
Kaljo, D. 1951. Nõukoguliku evolutsioonilise paleontoloogia meetodite rakendamine perekond *Vellamo* uurimisel. Tartu (manuscript, Institute of Geology, University of Tartu).
Laurie, J. R. 1991. Articulate brachiopods from the Ordovician and Lower Silurian of Tasmania. In *Australian Ordovician Brachiopod Studies* (Jell, P. A., ed.). *Mem. Ass. Australas. Palaeontols.*, **11**, 1–106.
Mitchell, W. I. 1977. *The Ordovician Brachiopoda from Pomeroy, Co. Tyrone. Palaeontogr. Soc. Monogr. Lond.*, **130**, 545.
Murchison, R. J., de Verneuil, E. & de Keyserling, A. 1845. *Geologie de la Russie d'Europe et des montagnes de l'Oural. Paleontologie,* **2**. Londres–Paris.
Nasedkina, V. A. 1970. Predstaviteli roda *Vellamo* v ordovikskikh otlozheniyakh zapadnogo sklona Urala. In *Materialy po paleontologii Urala* (Breivel, I. A. & Papulov, G. N., eds.). Akad. Nauk. SSSR, Uralskij Filial, Sverdlovsk, 43–51 (in Russian).
Nasedkina, V. A. 1973. Brakhiopody. In *Stratigrafiya i fauna ordovika Srednego Urala* (Varganov, V. G., Antsygin, N. Ya., Nasedkina, V. A., Militsina, V. S. & Shurygina, M. V., eds.). Nedra, Moskva, 111–142 (in Russian).
Öpik, A. 1930a. *Brachiopoda Protremata der estländischen ordovizischen Kukruse-Stufe. Publ. Geol. Inst. Univ. Tartu*, **1.**
Öpik, A. 1930b. *Beiträge zur Kenntnis der Kukruse-(C_2- C_3-) Stufe in Eesti, IV. Publ. Geol. Inst. Univ. Tartu*, **24**.
Öpik, A. 1934. *Über Klitamboniten. Publ. Geol. Inst. Univ. Tartu*, **39.**
Oradovskaya, M. M. 1977. Brakhiopody srednego ordovika Chukotskogo poluostrova. In *Stratigrafiya i fauna ordovika i silura Chukotskogo poluostrova* (Obut, A. M., ed.). *Tr. Inst. Geol. Geofiz. (Novosibirsk)*, **351**, 91–93 (in Russian).
Pahlen, A. 1877. *Monographie der baltisch-silurischen Arten der Brachiopoden-Gattung Orthisina. Mém. Acad. Sci. St.-Pétersb.*, Ser. **7**, 24, 8.
Raymond, P. E. 1921. *A Contribution to the Description of the Fauna of the Trenton Group. Geol. Surv. Can. Mus. Bull.*, **31**.
Schimer, H. W. & Schrock, R. R. 1955. *Index Fossils of North America.* New York.
Schuchert, C. & Cooper, G. A. 1932. *Brachiopod Genera of the Suborders Orthoidea and Pentameroidea. Peabody Mus. Nat. Hist. Mem., New Heaven*, **4**, 1.
Shaler, N. S. 1865. List of Brachiopoda from the Island of Anticosti. *Bull. Mus. Comp. Zool. Harvard*, **1**, 4, 61–70.
Sheehan, P. M. 1987. Late Ordovician (Ashgillian) brachiopods from the region of the Sambre and Meuse Rivers, Belgium. *Bull. Inst. R. Sci. Nat. Belg. Sci. Terre*, **57**, 5–81.
Termier, H. & Termier, G. 1950. Contribution a l' Étude des Faunes Paléozoïques de L'Algérie. *Bull. Serv. Carte Géol. Algér., Trav. Lab. Géol. Fac. Sci. Alger.*, **1**, 11, 11–52.
Tsegelnyuk, P. D. 1976. *Brakhiopody i stratigrafiya nizhnego paleozoya Volyno-Podolii.* Nauka, Kiev (in Russian).
Twenhofel, W. H. 1927. *Geology of Anticosti Island. Mem. Geol. Surv. Can.*, **154**. F. A. Ackland, Ottawa.
Williams, A. 1963. *The Caradocian Brachiopod Faunas of the Bala District, Merionetshire. Bull. British Mus. (Nat. Hist.) Geol.*, **8**, 7.
Williams, A. & Wright, A. D. 1965. Orthida. In *Treatise on Invertebrate Paleontology Brachiopoda, H.* (Moore, R. C., ed.). Univ. Kansas Press & Geol. Soc. Am., Lawrence, H299–H359.
Wilson, A. 1946. Brachiopoda of the Ottawa Formation of the Ottawa–St. Lawrence Lowland. *Bull. Geol. Surv. Can.*, **8**, 114–129.
Wright, A. D. 1964. The Fauna of the Portrane Limestone, II. *Bull. British Mus. (Nat. Hist.) Geol.*, **9**, 6, 241–256.

Wright, A. D. 1981. The external surface of *Dictyonella* and other pitted brachiopods. *Palaeontology*, **24**, 3, 443–481.
Wright, A. D. & Rubel, M. 1996. A review of the morphological features affecting the classification of clitambonitidine brachiopods. *Palaeontology*, **39**, 1, 53–75.

ORDOVIITSIUMI BRAHHIOPOODIPEREKOND *VELLAMO* EESTIS

Oive TINN

Ordoviitsiumi brahhiopoodiperekond *Vellamo* Öpik, 1930 on Eestis esindatud 16 liigiga. Teadaolevalt vanim on *V. pyramidalis* Pahlen, mis stratigraafiliselt levib Aserist kuni Haljala lademeni. Paralleelselt eelmisega on alates Lasnamäe lademest teada *V. parva* Öpik'u esinemine. Mõlemad kuuluvad väikeste kuni keskmiste, suhteliselt õhukese kojaga liikide hulka ning eristuvad rõõnestuse tiheduse poolest.

Suurima liigilise mitmekesisusega paistavad silma Haljala ja Keila lade, kus perekond *Vellamo* koosluse moodustavad üheksa, peamiselt keskmise kojasuurusega liiki. Sellel tasandil ilmuvad esimesed paksu koja ning nototüriaalse lava eesmise asetusega liigid *V. ambisulcata* Öpik ning *V. emarginata* Pahlen.

Pärast Keila aega on valdavad tihedalt üksteisele järgnevad, väikese stratigraafilise levikuulatusega liigid. Neile on iseloomulik keskmine kuni suur koda ning paks teisene kiht, mis mõningatel juhtudel (*V. verneuilii* Eichwald) täidab pediikli foraameni.

ОРДОВИКСКИЕ БРАХИОПОДЫ РОДА *VELLAMO* В ЭСТОНИИ

Ойве ТИНН

Ордовикские отложения Эстонии представлены 16 видами брахиопод рода *Vellamo* Öpik, 1930. По имеющимся данным, старейший из них – *V. pyramidalis* Pahlen – стратиграфически распространен от азериского до хальялаского горизонта. Параллельно последним, начиная с ласнамяэского горизонта, появляется *V. parva* Öpik. Оба вида имеют раковину размером от малого до среднего и отличаются друг от друга характером ребристости.

Наибольшим видовым разнообразием выделяются хальялаский и кейлаский горизонты, где род *Vellamo* представлен девятью видами, раковина которых среднего размера. На этом же уровне впервые встречаются виды с толстой раковиной и передним расположением на ней нототириальной платформы (*V. ambisulcata* Öpik и *V. emarginata* Pahlen).

Послекейлаские отложения содержат плотно следующие друг за другом, но с коротким стратиграфическим распространением виды. Для них характерны раковина размером от среднего до большого и толстый вторичный слой, который у некоторых экземпляров покрывает примакушечную часть раковины и форамен (*V. verneuilii* Eichwald).