Platystrophia (Orthida) and new related Ordovician and Early Silurian brachiopod genera

Michael A. Zuykov^a and David A. T. Harper^b

^a Department of Paleontology, St Petersburg State University, 29, 16 Liniya, 199178 St Petersburg, Russia; zuykov@riand.spb.su
 ^b Geological Museum, Øster Voldgade 5–7, DK-1350 Copenhagen, Denmark; dharper@snm.ku.dk

Received 27 December 2005, in revised form 18 September 2006

Abstract. More than 150 Ordovician and Early Silurian brachiopod species have been assigned to the genus *Platystrophia* King, 1850 mainly on the basis of their *Spirifer*-like shell exteriors. King's concept of the genus was based on *Platystrophia biforata* King, which is not conspecific with *Terebratulites biforatus* Schlotheim, traditionally regarded as the type species of *Platystrophia. Porambonites costatus* Pander, 1830 is formally proposed as the type species of the genus to replace *P. biforata*; the latter is considered to be a *nomen dubium*. In our revised diagnosis, *Platystrophia* is restricted to a group of Arenig to upper Caradoc species from Baltica and Avalonia, whereas the Ashgill and lower Silurian taxa of these regions, hitherto assigned to *Platystrophia*, are placed in the new genus *Neoplatystrophia*. *Platystrophia ponderosa* Foerste, 1909 from the Upper Ordovician of North America is proposed as the type species of a new genus *Vinlandostrophia*. Two new species, *Platystrophia baltica* and *Platystrophia pogrebovi* from the Llanvirn–Caradoc of the East Baltic are also described.

Key words: Rhynchonelliformea, Platystrophiidae, Baltica, Avalonia, Laurentia, new taxa.

INTRODUCTION

"The name *Platystrophia* proposed by Dr. King, has come into very general use for a group of orthids having a strikingly spiriferoid exterior" (Hall & Clarke 1892, p. 201).

Despite over a century of research on this group of orthide brachiopods, our current knowledge of the morphology and systematics of the many taxa assigned to "*Platystrophia*" remains poor. This is unfortunate since the *Platystrophia* plexus is one of the most distinctive brachiopod groups within the benthic faunas of the palaeocontinents of Baltica, Avalonia, and Laurentia during the Ordovician and Early Silurian. Two main problems have hindered our understanding of *Platystrophia*: (1) a misinterpretation of its genotype; and (2) generic assignment of taxa to *Platystrophia* and differentiation of its many species were based mainly on external characters, whereas the internal morphology of the majority of taxa has been neglected and remains unknown.

Here we revise the genotype of *Platystrophia* and describe in detail the morphology of some Baltic and Laurentian species previously assigned to the genus. We provide an emended diagnosis of the genus *Platystrophia* and a description of two new genera, *Neoplatystrophia* and *Vinlandostrophia*, from the Upper Ordovician and lower Silurian of Baltica and from the Upper Ordovician

of Laurentia, respectively. Both are externally similar to *Platystrophia*, but have distinctive, contrasting dorsal interiors. Two new *Platystrophia* species are proposed here for taxa from the Upper Ordovician of Baltoscandia (Fig. 1A,B), previously described or listed as "*Platystrophia biforata* Schlotheim, 1820" and "*P. lynx lynx* Eichwald, 1830", respectively. The stratigraphical ranges of these new species are shown in Fig. 1C. The morphology of the *Platystrophia*-like genera *Gnamptorhynchos* Jin, 1989 and *Siljanostrophia* Zuykov & Egerquist, 2005 from the Ashgill of Anticosti Island, Canada, and the Siljan district, Sweden, respectively, are also briefly discussed below.

MATERIAL AND METHODS

The material studied is from several sources.

 Museum collections. These institutions are listed below with the abbreviations used in the text: Central Scientific-Research Geological Exploration Museum (named after F. N. Chernyshev), St Petersburg (CNIGR); Museum of the Mining Institute, St Petersburg (MMI); Department of Paleontology, St Petersburg State University, St Petersburg (PMSPU); Institute of Geology at Tallinn University of Technology, Tallinn (GIT, collection 525); Department of Palaeozoology, Swedish Museum of Natural History (Riksmuseet),

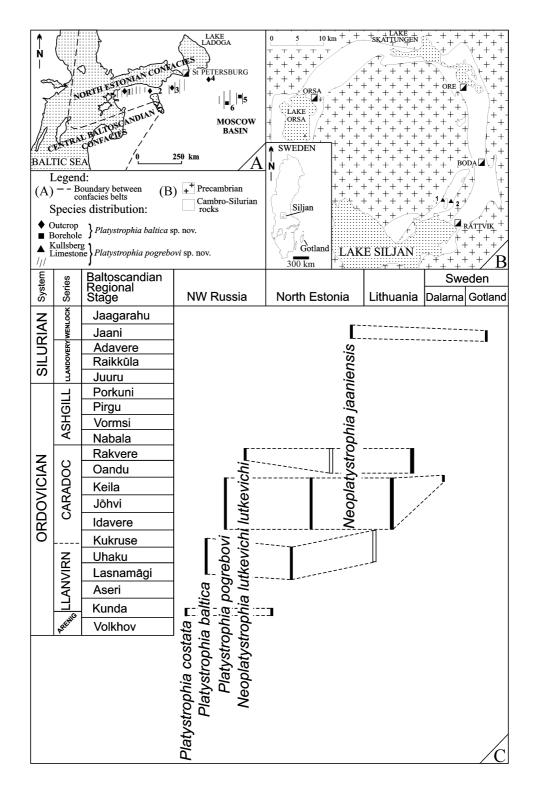


Fig. 1. (A), (B) Maps showing localities of new species of the genus *Platystrophia* described in this paper: (A) 1, Tallinn; 2, Kohtla-Järve; 3, Alekseevka; 4, Volkhov River; 5, Pestovo drill core; 6, Valdai drill core. (B) 1, Amtjärn; 2, Kullsberg. (C) Stratigraphical distribution of species described herein; black lines, data obtained by the authors, and white lines, data from Rõõmusoks (1970) and Paškevičius (1997). Correlation of the Ordovician and Silurian units in NW Russia, North Estonia, Lithuania, and Sweden are from Jaanusson (1982), Nõlvak (1997), and Paškevičius (1997).

Stockholm (SMNH); National Museum of Wales, Cardiff (NMW); The United States National Museum, Washington, DC (USNM); Peabody Museum of Natural History, Yale University, New Haven (YPM); Geological Survey of Canada, Ottawa (GSC).

- Specimens of *Platystrophia*-like brachiopod sampled by J. Paškevičius from cores in Lithuania and now housed in the Department of Geology and Mineralogy, Vilnius University, Lithuania.
- Collection made by R. Fine, J. Tate and other members of the Association of Amateur Geologists and Fossil Collectors, Dry Dredgers Inc., University of Cincinnati, and now housed in PMSPU.
- Important specimens donated to authors by Drs T. N. Alikhova, L. Hints, H. Leipnitz, V. A. Nasedkina, J. L. Benedetto, P. V. Fedorov, L. Popov, and S. S. Terentiev.
- 5. A large collection made by M. Zuykov for his doctoral thesis and housed in the CNIGR museum and PMSPU.

In general, more than 4000 specimens of Platystrophia-like brachiopods have been studied from the Ordovician to Early Silurian of Argentina, Canada, Estonia, Germany, Ireland, Lithuania, NW Russia, Sweden, Ukraine, UK, and the USA. Since many of the studied Platystrophia-like brachiopods are represented only by conjoined valves, transverse serial sections were necessary to investigate their internal structures. For the first time these brachiopods have been sectioned at angles between 30° and 40° to the lateral commissure (Fig. 2B,E–G), providing more information than that available previously. For comparative purposes serial sections perpendicular to the lateral commissure were also examined. Disarticulated dorsal valves embedded in dental plastic were excavated mechanically to expose the cardinalia, critical for their classification. Latex casts of internal moulds were also studied where possible. Unfortunately not all specimens could be investigated internally; irreplaceable museum specimens, for example, lack data on their internal structures and are not discussed further.

It is important to note that spinose ornamentation (or even granulation) is usually absent on type material of previously described taxa, not only due to shell exfoliation, but often because techniques used to clean the specimens from sediment have eradicated these important features. Thus some taxa can only be tentatively assigned to the *Platystrophia*-like group of brachiopods.

REMARKS ON THE CONCEPT OF *PLATYSTROPHIA* KING, 1850

For many years the genotype of *Platystrophia*, "*Terebratulites biforatus* Schlotheim, 1820" was regarded

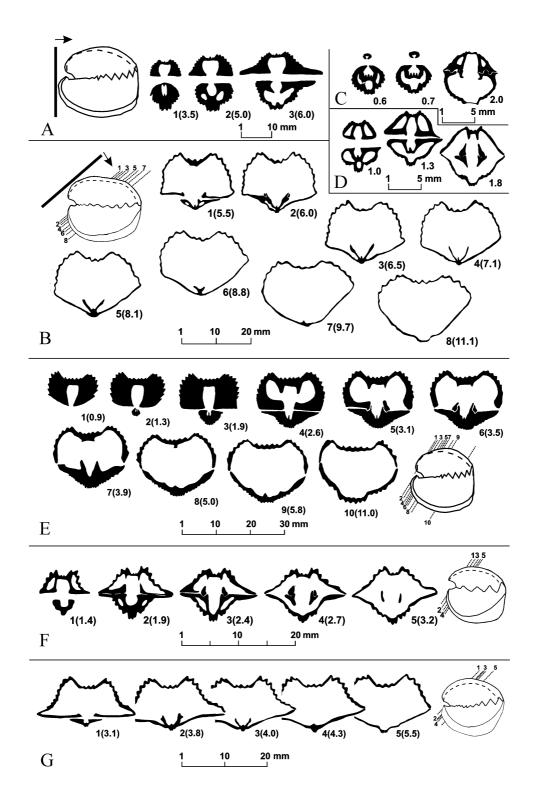
as a Spirifer-like taxon with five costae in the ventral sulcus, six on the dorsal fold and nine on the flanks of both valves; its age and locality was commonly referred to as "the Ordovician of the Baltic area (exact locality and horizon uncertain)" (Cocks 1978, p. 55) or "Ordovician, from the erratic boulder of North Germany" (Alikhova 1960, p. 186). In fact, a typical Platystrophia-like brachiopod from the Upper Ordovician of North America (Cincinnati, Ohio), with initially a triplicate costal condition in the sulcus, was referred to "P. biforata (Schlotheim)" as a type species of the genus *Platystrophia* in the Treatise on Invertebrate Paleontology (Williams & Harper 2000), a proposal supported by other brachiopod workers (L. R. M. Cocks pers. comm.). Although this provided some stability for the genus, this approach had already been criticized by Bather (1920, p. 89) and Dietrich (1922, p. 123). Moreover, none of those specimens from North America was referred to "P. biforata" subsequent to Schuchert & Cooper (1932), although that had been common practice prior to their substantial monograph (Schuchert 1897, p. 309).

Under the International Commission on Zoological Nomenclature Rules (ICZN 1999, Articles 11.10 and 69.2.4) the formally designated type species of *Platystrophia* is *P. biforata* King, 1850. King (1850, p. 106, in the previous paragraph to the description of *Platystrophia*), deliberately based his definition of the genus on specimens of *Orthis biforata "sensu*" Davidson, 1848. Therefore, the type species of the genus is from the "Wenlock limestone of Walsall" (Davidson 1848, p. 323) in the vicinity of Birmingham; this unit is now referred to the Much Wenlock Limestone Formation of mid Silurian age (Bassett et al. 1975).

However, the original specimens of *P. biforata* King, 1850 (= *O. biforata*) described by Davidson (1848, p. 323, pl. III, fig. 25) are lost, and there are no other originals in the type series housed in the Natural History Museum, London, or elsewhere (Dr L. R. M. Cocks and Dr L. E. Popov pers. comm.).

Bassett (1972, p. 32, pl. V, figs 3–5) described a few specimens from the Wenlock of Walsall as *Platystrophia* sp. A and included specimens of *O. biforata* described by Davidson (1848, 1871) in his synonymy list for that species. There were no satisfactory data on the morphological features of *O. biforata* given in the description or shown in the figures in Davidson's monograph (1848, p. 323), which allow the unequivocal assignment of any specimens from the Wenlock Limestone of Walsall to *P. biforata* (King, 1850). Thus, there are no strong grounds to either confirm or reject the assumption that Bassett (1972, p. 32) described and illustrated specimens conspecific with *P. biforata* King, although they came from the type locality and unit. In 1871, Davidson (p. 268) figured some additional specimens from the Caradoc and Wenlock of Britain and Ireland under the name *Orthis biforata*; however, this material is also lost. None of that material is conspecific with the material figured in the original publication by Davidson (1848, p. 323, pl. III, fig. 25). It is thus concluded, herein, that without a restudy of the original specimens, "*P. biforata* King, 1850" must be considered a *nomen dubium*.

In general, however, King's (1850) diagnosis represents a clear morphological concept, which can be applied



to most of the species presently referred to the genus. For instance, he recorded the presence of "large punctures" (which were later interpreted as "granules", but in reality represent the remains of hollow spines) on the external shell surface. Therefore, the presence of this feature, which is otherwise unknown among brachiopods of the order Orthida, must be diagnostic of the type species of *Platystrophia*. King, apart from discussing the type species, included four other species in Platystrophia (King 1850, p. 106): Spirifer tscheffkini Verneuil (1845), Porambonites dentatus Pander (1830), Porambonites costatus Pander (1830), and Spirifer terebratuliformis M'Coy (1846). Apart from the first species, which has since been assigned to the unrelated pentameride genus Noetlingia (Hall & Clarke 1893, p. 229), the other three define a distinct morphological group which can be included within *Platystrophia*. Since the concept of Porambonites costatus Pander is clearly defined, we recently suggested (Zuykov & Harper 2004) that this species should be designated as the type species of Platystrophia. Platystrophia costata (Pander, 1830) has been revised recently by Zuykov (1999, p. 200), and the neotype from Pander's collection has been chosen for this species. This has been accepted by the International Commission on Zoological Nomenclature, Opinion 2154 (ICZN 1999, Case 3290).

REMARKS ON THE CARDINALIA IN PLATYSTROPHIID BRACHIOPODS

Seven morphological terms are commonly used in the description of platystrophild cardinalia: brachiophores, brachiophore plates, sockets, fulcral plates, cardinal process, notothyrial platform, and sessile septalium. In general, we follow the terminology used by Williams & Brunton (1997; see also discussion in Brunton et al. 1996), but some of these terms have not always been used consistently and may have contributed to misinterpretations of the morphology of the platystrophild brachiopods.

Brachiophore or brachiophore plates?

Two separate terms "brachiophore" and "brachiophore plates" are in common usage (e.g. Schuchert & Cooper 1932; Williams et al. 1965; Williams & Brunton 1997), but difficulties in often distinguishing brachiophores and brachiophore plates in a range of different brachiopod groups have contributed to a rather flexible use of these terms, in a number of different circumstances, e.g. according to systematic rank (see discussion in Brunton et al. 1996), mode of preservation, the growth stage of the studied specimens or even when used for comparative purposes (Lazarev 1976). This makes comparisons between platystrophiid taxa difficult, because of the lack of clarity of definition and understanding of these and other associated structures (fulcral plates, sessile septalium, notothyrial platform). For example, this is probably one of the reasons why differences between the cardinalia of brachiopods in the European and North American representatives of the genus Platystrophia (s.l.), which we assign here to different types of cardinalia following Schuchert & Cooper (1932), have never been discussed earlier.

Schuchert & Cooper (1932, p. 37) proposed the terms "brachiophores" and "brachiophore plates" for "the structures on either side of the notothyrium which bound the sockets and to which was attached the elongate brachiophore process; to the latter in turn was fastened the lophophore. In some genera the brachiophores are supported dorsally by plates, and to these the name brachiophore plates or support is given." This is supplemented by further morphological characters, together distinguishing ten "types of brachiophores" (1932, pp. 37–39). It is significant that these types differ not only with respect to the brachiophores themselves, but also with reference to the presence or absence of fulcral plates and notothyrial platforms. Thus, in Schuchert and Cooper's monograph discrimination between a wide range of various "types of cardinalia" was possible.

Fig. 2. Transverse serial sections of *Platystrophia*-like brachiopods. (A), (B) *Vinlandostrophia ponderosa* (Foerste, 1909) with indication of directions of sections: (A) traditional orientation, based on specimen PMSPU 41-6; (B) orientation recommended here, based on specimen CNIGR 41-1, McMillian Formation, Maysville, Upper Ordovician, near Hamilton, Butler County, Ohio, USA. (C) *Gnamptorhynchos globatum* (Twenhofel, 1928), based on the specimen illustrated by Jin & Zhan (2000, fig. 5), GSC 102449, from the Prinsta Member, Ellis Bay Formation, Ashgill, Lousy Cove, Anticosti Island, Canada. (D) *Siljanostrophia jaanussoni* Zuykov & Egerquist (2005), CNIGR 10/13121, Boda Limestone, Ashgill, Osmundsberget Quarry, Siljan district, Dalarna, Sweden. (E) *Platystrophia baltica* sp. nov.; CNIGR 3/13122, Kukruse Stage, Viivikonna Formation, Kohtla-Järve, Estonia. (F) *Neoplatystrophia jaaniensis* (Rubel, 1963); CNIGR 11/13126, Visby Formation, lower Silurian, Gotland, Sweden. (G) *Vinlandostrophia acutilirata* (Conrad 1842); CNIGR 41-4, Waynesville Formation, Richmond, Upper Ordovician, near Spring Valley, Greene County, Ohio, USA.

The distance in mm is measured from the tip of the ventral beak; dorsal valve lowermost. Lateral view to show section positions.

By contrast, in the glossary of morphological terms in the Treatise, the authors (Williams et al. 1965; Williams & Brunton 1997) argued that the brachiophore plates are the basal (dorsal) parts of brachiophores that join the floor of valve. We agree with Williams & Wright (1963), Lazarev (1976) and others that there are no differences between the character of secondary shell comprising the brachiophores and brachiophore plates; they form a single structure. Consequently, only one term is necessary to limit confusion in the description and understanding of the morphology of cardinalia. We suggest that only the term "brachiophore" is used for his element of the cardinalia as originally proposed by Schuchert & Cooper (1932). There are no difficulties with the description of shape, size, and direction of various parts of the brachiophore (e.g. basal part), whereas the term "brachiophore plates" as defined in the revised Treatise (Williams & Brunton 1997) is not followed here. This strategy is followed for the Platystrophia-like brachiopods described and discussed here; a similar strategy may be relevant for other, morphologically similar brachiopod groups (see discussion in Brunton et al. 1996).

Septalium and sessile septalium

In general, the septalium is a trough-shaped structure in the umbonal region of the dorsal valve. There have been various opinions on the terminology, morphology, and taxonomical significance of this structure. According to the glossary of morphological terms in the *Treatise* (Williams & Brunton 1997), a septalium is defined as the "troughlike structure of dorsal valve between crural bases, consisting of crural plates (or homologues) fused medially and usually supported by a median septum, but may be unsupported or sessile; does not carry adductor muscles". Brunton et al. (1996, p. 21) noted that in cross-section, septalia have a typical Y-shape, but when the cross-section is V-shaped, they suggest the use of the term "sessile septalium".

Schuchert & Cooper (1932, p. 66) were first to use the term "sessile cruralium" (= sessile septalium) during their discussion of the dorsal cardinalia of the genus *Platystrophia* (s.l.). Subsequently, however, this term was used only in the two editions of the *Treatise* (Williams & Wright 1965; Williams & Harper 2000, p. 775) in the diagnosis of the genus *Platystrophia* and the family Platystrophiidae ("bladelike brachiophores joined to hinge line by concave fulcral plates and supported by plates converging posteromedianly to form small septalium"). But other workers have very rarely used this term even in descriptions of North American *Platystrophia*-like brachiopods, where this term seems to be more applicable. For example, in his substantial review of the *Platystrophia* (s.l.) from the Upper Ordovician of Kentucky, Alberstadt (1979) only once, when describing the cardinalia of *Platystrophia ponderosa* (= *Vinlandostrophia ponderosa*), used the term "septalium-like structure". Our study of that species from numerous specimens with different degrees of preservation and at different growth stages clearly suggests that the term "sessile septalium" can be readily applied to the cardinalia of *V. ponderosa*, where it is characterized by a clear V-shaped form in cross-section (Fig. 2B; Pl. II, figs 19, 20).

However, there are some differences in the cardinalia of other species assigned here to *Vinlandostrophia* as well as in species of *Neoplatystrophia*. These taxa lack a clear V-shaped septalium, but have a more U-shaped structure in cross-section, which is formed by the convergence of thin brachiophores (Figs 2F,G, 3; Pl. II, figs 7, 8, 10, 13–15). Because of the division of the umbonal cavity into three parts, as in the case of the V-shaped sessile septalium, we have termed this structure a sessile septalium. This same term has been used for the sessile septalium of some athyridid and rhynchonellid brachiopods (e.g. Sartenaer 1969, 1970; Grunt 1989; Erlanger 1994; Alvarez & Carlson 1998; Alvarez & Brime 2000; Savage et al. 2002; Alvarez & Rong 2002).

Notothyrial platform

According to the terminology of the *Treatise* (Williams & Brunton 1997), a notothyrial platform is defined as the "umbonal thickening of floor of dorsal valve between inner socket ridges, brachiophore, or crural plates". Schuchert & Cooper (1932, pp. 37–39) reported the presence of notothyrial platforms in both the Billingsellidae and Orthidae. We agree with Schuchert and Cooper's conclusion that the notothyrial platform is absent in some Plectorthoidea, where a sessile septalium

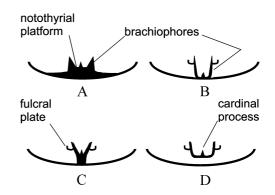
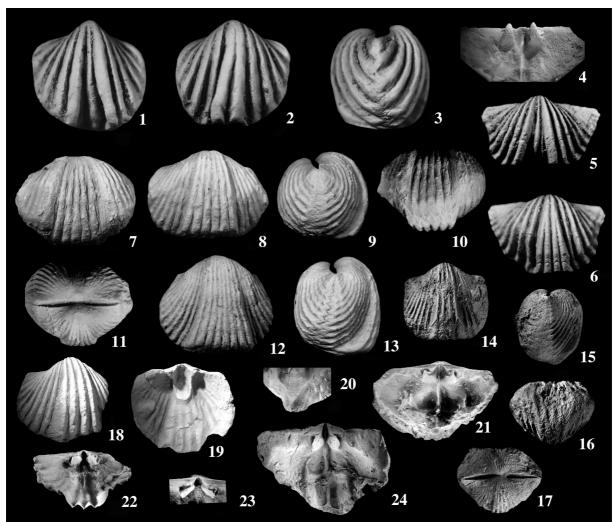


Fig. 3. Scheme showing the different types of cardinalia in *Platystrophia*-like brachiopods as discussed herein. (A) *Platystrophia* King; (B) *Neoplatystrophia* gen. nov.; (B),(C) *Vinlandostrophia* gen. nov.; (D) *Siljanostrophia* Zuykov & Egerquist, *Gnamptorhynchos* Jin.





Explanation of Plate I

- Figs 1–6. *Platystrophia costata* (Pander, 1830); 1–3, ventral, dorsal, and lateral views of neotype (MMI 1/373), Pulkovka River, St Petersburg region, Russia; ×3. 4, dorsal valve interior view (CNIGR 12/13121), Upper Arenig, Obukhovo Formation, Kunda Stage, Putilovo quarry, St Petersburg region, Russia; ×3. 5, 6, ventral and dorsal views (CNIGR 6/12974), Upper Arenig, Obukhovo Formation, Kunda Stage, Putilovo quarry, St Petersburg region, Russia; ×2.
- Figs 7–13. Platystrophia baltica sp. nov.; 7–11, ventral, dorsal, lateral, anterior, and posterior views of holotype (CNIGR 1/13122), Lower Caradoc, Viivikonna Formation, Kukruse Stage, Alekseevka quarry, St Petersburg, Russia; ×1. 12, 13, dorsal and lateral views (CNIGR 2/13122), Lower Caradoc, Viivikonna Formation, Kukruse Stage, Alekseevka quarry, St Petersburg, Russia; ×1.
- Figs 14–21. Platystrophia pogrebovi sp. nov.; 14–17, dorsal, lateral, anterior, and posterior views of holotype (CNIGR 5/13126), Lower Caradoc, Kahula Formation, Jõhvi Stage, Aluvere quarry, Estonia; ×1. 18, dorsal valve view (SMNH Br. 102447), Lower Caradoc, Kullsberg Limestone, Kullsberg quarry, Siljan district, Dalarna, Sweden; ×1.5. 19, ventral valve interior view (SMNH Br. 102458), Lower Caradoc, Kullsberg Limestone, Kullsberg quarry, Siljan district, Dalarna, Sweden; ×1.5. 20, ventral valve interior view, anterior slope of the muscle field (PMSPU 41-7), Lower Caradoc, Gryazno Formation, Ojamaa Substage, Idavere Stage, Klyasino quarry, St Petersburg region, Russia; ×1.5. 21, dorsal interior view (CNIGR 3/13042), Lower Caradoc, Gryazno Formation, Ojamaa Substage, Idavere Stage, Klyasino quarry, St Petersburg region, Russia; ×1.5.
- Figs 22, 23. *Platystrophia lata* Alichova (1951), dorsal valve interior view and cardinalia (CNIGR 2/13042), Gryazno Formation, Idavere Stage, Lower Caradoc, Klyasino quarry, St Petersburg region, Russia; ×1.5, ×2.
- Fig. 24. ?*Platystrophia* sp.; latex cast of internal mould of dorsal valve (NMW 73.3g.5348), Gelli-grin Formation, Longvillian, Middle Caradoc, Bala district, UK; ×1.5.

(see above) is commonly developed (1932, p. 39). Although *Platystrophia* (*s.l.*) was assigned to the Plectorthidae, the term "notothyrial platform" was used in the description of their cardinalia, even for forms with sessile septalia. This has, however, caused difficulties in the description of such cardinalia where adequate illustrations are lacking. Thus, in this paper we apply the term "notothyrial platform" for the description of cardinalia in *Platystrophia* (*s.s.*), whereas in *Neoplatystrophia* and *Vinlandostrophia* this term is not used because sessile septalia are developed.

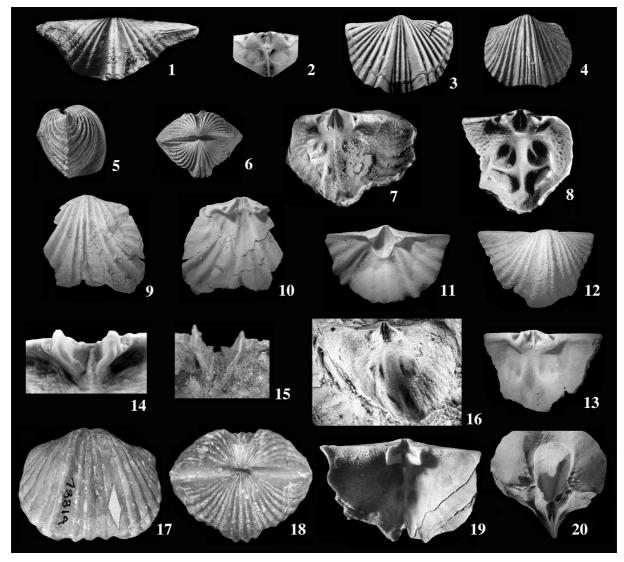
REMARKS ON MORPHOLOGY

Origination of costae in the median sulcus

Although the radial ornament of *Platystrophia* is one of its most distinctive features, its taxonomic significance

is not well understood (see also discussion in Sinclair 1946; Williams 1962, 1963; Wright 1964). Nevertheless, assignment of individual species of Platystrophia (s.l.) to (1) uniplicate (Pl. I, figs 1, 2; Pl. II, fig. 1), (2) biplicate (Pl. I, figs 7-19) or (3) triplicate (Pl. II, figs 17-20; Pl. III, figs 1-4) groups after Cumings (1903, p. 10) is generally clear cut. Moreover, Cumings's assumption that the difference between North American (Laurentian) and European (Baltoscandian, Avalonian) taxa can be based on their assignment to triplicate or biplicate types, respectively, is broadly supported here. No species with a triplicate ornament is known in our collections from Baltoscandia and Avalonia apart from four specimens, one of which is illustrated (Pl. I, figs 5, 6). These specimens, from the upper Arenig of the St Petersburg region, are characterized by a radial ornament that closely resembles the uniplicate Platystrophia costata; however, anterior to mid-valve the St Petersburg species develops





features of the triplicate group. Some specimens of P. costata, however, have an additional bifurcating rib in the ventral sulcus and on the dorsal median fold. The interiors of these specimens are, nevertheless, similar to more typical forms. Three interpretations are possible: 1) the more aberrant specimens of *P. costata* are not the result of population variation, but mark the welldeveloped exterior of a separate intraspecific group; 2) the most complicated "triplicate" mode of origin of costae in the ventral sulcus was tested in the "Platystrophia group" at an early stage in its evolution, but it was positively selected for only in the Late Ordovician; 3) it may indicate, indirectly, probable early relationships between the Baltoscandian and Laurentian Platystrophia-like genera. The last is, in our opinion, most probable.

North American biplicate species are not considered in the present paper because of poor knowledge of their internal morphology. Nevertheless, the morphology of such forms has been studied in two species from the Charles Schuchert collection, housed in the Peabody Museum. These Early Silurian taxa, identified by Schuchert as "*Platystrophia reversata* (Foerste), Brassfield Fm, Ohio" and "*Platystrophia* sp., Manitoulin Formation, Ontario, Canada" have similar internal features to those of *Neoplatystrophia*; moreover, both show the similar origination of costae, with some representatives of the later genus characterized by the bifurcation of median costae anterior to mid-valve (e.g. *N. lutkevichi*).

Spinose ornamentation

The presence of thin, hollow spines or their bases, traditionally described as a granulose or pustulose microornament (Pl. III, figs 8–11) on the external surface of the shell (except interareas), was recorded in *Platystrophia* (*s.l.*) in the nineteenth century (e.g. King 1850; Hall & Clarke 1892). Fitzpatrick (1971) examined this ornament on *Platystrophia cypha* from the Upper Ordovician of North America; he measured the density of granulation (90–120 per 1 mm²), diameter (0.03– 0.065 mm), and lengths of single granules (0.15–0.2 mm). Our observations on the shell surface of some Upper Ordovician species from North America, assigned here to *Vinlandostrophia*, support Fitzpatrick's data. A similar type of spinose ornament (see Pl. III, fig. 8) is also

Explanation of Plate II

- Figs 1, 2. *Platystrophia crassoplicata* Alichova (1951); 1, dorsal valve view (GIT 523-13); ×1.5. 2, dorsal valve interior view (GIT 523-12); ×1.5. Both specimens are from the Upper Caradoc, Oandu Stage, Oandu River (near Rebu village), Estonia.
- Figs 3–7. Neoplatystrophia lutkevichi lutkevichi (Alichova, 1951); 3, ventral valve view of holotype (CNIGR 19/8047), Upper Caradoc, Rakvere Stage, Plyussa River, St Petersburg region, Russia; ×1.5. 4–6, dorsal, lateral, and posterior views (CNIGR 9/13126), Upper Caradoc, Hirmuse Formation, Rakvere Stage, Pechurki quarry, St Petersburg region, Russia; ×1. 7, dorsal valve interior view (CNIGR 10/13126), Upper Caradoc, Hirmuse Formation, Rakvere Stage, Pechurki quarry, St Petersburg region, Russia; ×1.5.
- Fig. 8. Neoplatystrophia sp.; dorsal valve interior view (GIT 525-17), (?) Nabala Stage, Ashgill, Viru-Jaagupi, Estonia; ×1.
- Figs 9–11. *Neoplatystrophia jaaniensis* (Rubel, 1963); 9, 10, dorsal valve, exterior and interior views (SMNH Br. 115710), Visby Formation (lower Silurian), Gotland, Sweden; ×2. 11, ventral valve interior (SMNH Br. 115711), Visby Formation (lower Silurian), Gotland, Sweden; ×2.
- Figs 12, 13. *Neoplatystrophia* sp.; dorsal valve, exterior and interior views (SMNH Br. 138041), Kõrgessaare Formation, Vormsi Stage, Ashgill, Hiiumaa Island, Estonia; ×2.
- Fig. 14. *Neoplatystrophia quadriplicata* (Alichova, 1951); dorsal valve interior view (PMSPU 42-34), Upper Caradoc, Rakvere Stage, Plyussa River, St Petersburg region, Russia; ×6.
- Fig. 15. ?*Neoplatystrophia lutkevichi contemplata* (Wright); dorsal valve interior view (USNM, no number has been given), Portrane Limestone, middle Ashgill, County Dublin, Ireland; ×4.
- Fig. 16. ?*Neoplatystrophia* sp.; latex cast of internal mould of dorsal valve (NMW 77.11g.182), Pen-y-garnedd Formation, Woolstonian, Upper Caradoc, Berwyn hills, UK; ×1.5.
- Figs 17–20. *Vinlandostrophia ponderosa* (Foerste, 1909); 17, 18, ventral and posterior views of holotype (USNM 78814), Bellevue Member, Maysvillian, Upper Ordovician, Madison, Indiana, USA; ×0.9. 19, dorsal valve interior view (YPM S-556A), Upper Ordovician, Cincinnati, Ohio, USA; ×0.9. 20, incomplete conjoined valves, interior view (SMNH Br. 86752), Maysvillian, Upper Ordovician, west Chester, Ohio, USA; ×1.

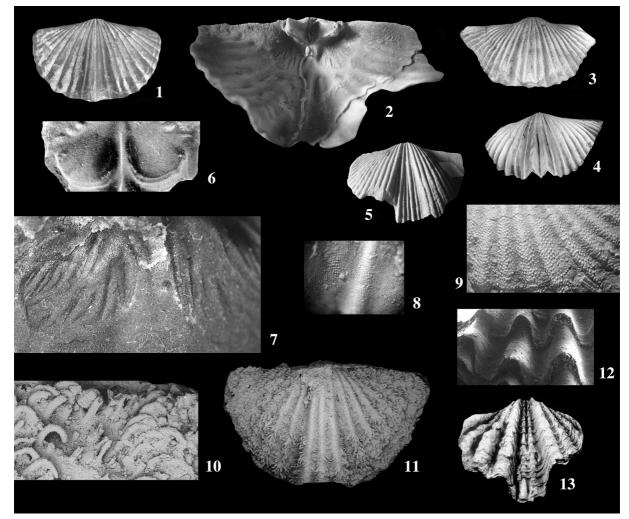
recorded in Ashgill *Neoplatystrophia*, *Siljanostrophia*, and, probably, *Gnamptorhynchos* Jin (1989) (Jin Jisuo, pers. comm. 2001). However, in *Platystrophia* (*s.s.*) the density and diameter of granulation are halved, comprising 45–60 per mm² and 0.05–0.08 mm, respectively (Pl. III, figs 9–11). All these measurements (e.g. those given in palaeontological descriptions) have been made by authors in the slope of sulcus at mid-valve length. Although this difference may be a useful diagnostic feature to distinguish the genus *Platystrophia* from the three other genera discussed above, it needs to be evaluated statistically on larger sample sizes of each genus at various growth stages.

Well-preserved spines are observed on specimens of *Platystrophia lata* Alichova and *P. pogrebovi* sp. nov. from the lower Caradoc of the St Petersburg region (Pl. III, figs 10, 11). As shown on the illustrations, these spines are relatively large (about 1 mm in diameter) and curve at about mid-length with their distal ends facing down (i.e. "hook-shaped" spines). The nature of the spines on most *Platystrophia* species remains unknown. The spines on unfigured specimens of *Neoplatystrophia* and *Vinlandostrophia* are nearly orthogonal and inclined towards the anterior margin.

Another type of distinctive ornament is observed on shells which are traditionally assigned to *Platystrophia chama* Eichwald and *P. caelata* Williams. It is characterized by strongly developed frilly growth lamellae extending along the crests of the costae. However, no spines or remains of spines (e.g. granulations, pits, etc.) have been observed even on well-preserved specimens of *P. chama* (Pl. III, figs 12, 13). The frilly lamellae and spines may have functioned to discourage fouling by epibionts (Alvarez & Taylor 1987; Alexander 2001).

Neuman (1976, p. 22) noted that "granular or spinose surfaces are so characteristic of *Platystrophia*, that similar forms having a smooth surface probably should be put in a different genus". We agree with Neuman's opinion, and here we only tentatively assign taxa lacking any kind of micro-ornament to the genera discussed below.

PLATE III



Cardinalia

The classic investigation of orthide cardinalia remains that of Schuchert & Cooper (1932) whose diagnosis (p. 66) of *Platystrophia* (s.l.) includes the following: "The interior of *Platystrophia* links the genus intimately to Plectorthis and Hebertella, as best seen in young specimens." It also says: "In the dorsal valve the brachiophores and their supporting plates are not divisible. The combined plates converge to form a sessile cruralium." Thus, this type of cardinalia was described (ibid, p. 38) as the "(4) Plectorthis-Hebertella type". Consequently, Platystrophia (s.l.) was traditionally placed within the Plectorthidae, an assignment followed in the *Treatise* and many frequently-quoted papers, e.g. Williams & Wright (1965) and Williams & Harper (2000). However, Schuchert and Cooper observed that the variation of the shape of the sessile septalium in cross-section can be documented in Upper Ordovician species, now assigned to Vinlandostrophia and Neoplatystrophia (Figs 2, 3; Pl. II, figs 7, 14, 20); the sockets are confined by fulcral plates.

A further type of cardinalia is developed in *Platy-strophia costata* (Pander, 1830) and other Arenig to late Caradoc species from Baltoscandia and Avalonia are assigned here to the genus *Platystrophia* (*s.s.*). This

cardinalia is characterized by disjunct thick brachiophores of various shapes (e.g. pyramidal, subtriangular, blade-like), with thick basal parts that swell out from the notothyrial platform (Figs 2, 3; Pl. I, figs 4, 21–24).

Data published recently by Jin (1989), together with Jin & Zhan (2000), indicate a third type of cardinalia in *Platystrophia*-like brachiopods which is characteristic of *Gnamptorhynchos globatum* (= *Platystrophia regularis globata* Twenhofel, 1928) from the Ashgill of Anticosti Island. This type of cardinalia is characterized by accessory teeth in the ventral valve and a "trilobate" cardinal process (see below), situated on a platform which is free anteriorly and supported dorsally by two ridges (Fig. 2C). With the exception of some slight differences, the cardinalia of *G. globatum* resemble those of *Siljanostrophia jaanussoni* Zuykov & Egerquist (2005) from the Ashgill Boda Limestone of the Siljan district, Sweden (Fig. 2D).

Cardinal process

The cardinal process is a simple, generally narrow (blade-like) and prominent ridge in the centre of the notothyrial platform or on the floor of the dorsal valve, in the case of the species with a sessile septalium. The cardinal processes of the oldest known species of the genus *Platystrophia*, *P. costata* (Pander, 1830) and

Explanation of Plate III

- Figs 1, 2. *Vinlandostrophia laticosta* (Meek, 1873); 1, ventral valve view (PMSPU 41-5), Bellevue Member, McMillan Formation, Maysvillian, Upper Ordovician, Crestview Hills, Kenton County, Kentucky, USA; ×1. 2, dorsal valve interior view (YPM S-575C), Maysvillian, Upper Ordovician, Cincinnati, Ohio, USA; ×2.
- Fig. 3. *Vinlandostrophia acutilirata* (Conrad, 1842); dorsal valve view (PMSPU 41-8); Waynesville Formation, Richmond, Upper Ordovician, Greene County, Ohio, USA; ×1.5.
- Fig. 4. *Vinlandostrophia cypha* (James, 1874); dorsal valve view (PMSPU 42-24); Whitewater Formation, Richmond, Upper Ordovician, Brookville, Indiana, USA; ×0,9.
- Fig. 5. ?Neoplatystrophia reversata (Foerste); ventral valve view (YPM 206751); Brassfield Formation, Lower Silurian, Ohio, USA; ×1.2.
- Fig. 6. *Platystrophia pogrebovi* sp. nov.; dorsal valve interior view, posterior adductors (PMSPU 41-9), Gryazno Formation, Ojamaa Substage, Idavere Stage, Lower Caradoc, Klyasino quarry, St Petersburg region, Russia; ×3.5.
- Fig. 7. Vinlandostrophia ponderosa (Foerste, 1909); dorsal valve interior view (USNM 189467), Richmond, Upper Ordovician, Kentucky, USA; ×5.
- Fig. 8. Platystrophiidae gen. et sp. indet.; (SMNH Br. 138040), Kullsberg Limestone, Upper Caradoc, Siljan district, Dalarna, Sweden; ×5.
- Fig. 9. *Platystrophia pogrebovi* sp. nov.; dorsal valve view (CNIGR 3/13121), Kullsberg Limestone, Upper Caradoc, Kullsberg quarry, Siljan district, Dalarna, Sweden; ×4.
- Figs 10, 11. *Platystrophia lata* Alichova (1951); dorsal valve view (CNIGR 4/13121), Gryazno Formation, Ojamaa Substage, Idavere Stage, Lower Caradoc, Klyasino quarry, St Petersburg region, Russia; ×6, ×32.
- Figs 12, 13. ?*Platystrophia chama* Eichwald, 1861; ventral valve view (CNIGR 2/7135), Jõhvi Stage, Upper Caradoc, Aluvere quarry, Estonia; ×5, ×2.

P. putilovensis Zuykov (1999), extend anteriorly to meet a median septum that continues to the end of the muscle field as on Pl. I, fig. 4. The cardinal process is always present, but may vary in size. In *Neoplatystrophia* two small additional ridges may extend parallel to the cardinal process in some adult individuals (Pl. II, figs 7, 13). In addition, these ridges form part of the diagnosis of *Gnamptorhynchos globatum* (Twenhofel, 1928) where, however, the feature is known only from a few specimens (Fig. 2C). There are comparable structures in specimens in the Schuchert collection (Peabody Museum) identified here as *?Neoplatystrophia reversata* (Foerste), in which the additional ridges extended parallel to the cardinal process.

In their study of the clitambonitidine cardinal process Wright & Rubel (1996, pp. 63–64) concluded that the taxonomic significance of such ridges may be determined in each case only after statistical treatment of large samples. A similar argument applies here.

Adductor muscle field

The dorsal adductor field in genera with Platystrophialike exteriors is quadripartite. The anterior pair is smaller than the posterior pair or both pairs may be equidimensional. The outline of the adductors has been variously described for different species as oval, elongate ellipsoidal, circular, triangular or subrhomboidal. The anterior adductor scars are commonly poorly defined, while the posterior adductor scars are typically well impressed because of the slight thickening of secondary shell with distinctly pointed anterior ends. In Platystrophia and Vinlandostrophia, the anterior and posterior pairs are closely spaced in the central part of the dorsal valve (Pl. I, figs 4, 21, 24; Pl. III, figs 2, 6, 7). A low ridge or well-developed median septum bisects the adductor scars medially. Nevertheless, the width and height of the median septum between the posterior pair usually varies between species or even between individuals. In both young and adult individuals of Vinlandostrophia the impressions of the posterior adductors are covered by thin and low creases which are formed of secondary shell (Pl. II, fig. 19; Pl. III, figs 2, 7), whereas these scars in Platystrophia are completely smooth (Pl. III, fig. 6). Neoplatystrophia, Gnamptorhynchos, and Siljanostrophia (Fig. 2C,D; Pl. II, figs 7, 8, 10, 13, 16) have a marked gap between the posterior adductor scars, and the median septum is absent. Moreover, in well-preserved, thickshelled adult individuals of Neoplatystrophia, the posterior adductors are bisected by variously developed ridges (Pl. II, figs 7, 8, 13, 16). However, the shell is too thin in young individuals of Neoplatystrophia, and thus such detail of the posterior adductors cannot be observed. There are some *Platystrophia*-like species from the Upper Ordovician of North America that are somewhat similar to *Neoplatystrophia* with regard to this character (e.g. *P. reversata* and *Platystrophia* sp. from the Schuchert collection, see discussion above). Alberstadt (1973) also reported that the posterior adductor scars are bipartite in two species (*P. sutherlandi*, *P. uncinata*) from the Viola Formation of Oklahoma.

These examples demonstrate that the morphology of the posterior adductors is useful for generic discrimination. With some reservations, the bisection of each posterior adductor by ridges in the case of *Neoplatystrophia* may also be of taxonomic significance. However, the latter feature requires statistical analysis to test its efficacy. The key morphological features of the genera of *Platystrophia*-like brachiopods recognized herein are shown in Table 1.

SYSTEMATIC DESCRIPTIONS

Phylum BRACHIOPODA Dumeril, 1806 Subphylum RHYNCHONELLIFORMEA Williams et al., 1996 Class RHYNCHONELLATA Williams et al., 1996 Order ORTHIDA Schuchert & Cooper, 1932 Suborder ORTHIDINA Schuchert & Cooper, 1932 Superfamily PLECTORTHOIDEA Schuchert in Schuchert & LeVene, 1929 Family PLATYSTROPHIIDAE Schuchert in Schuchert & LeVene, 1929, emend.

Type genus. Platystrophia King, 1850.

Emended diagnosis. Dorsibiconvex with *Spirifer*-like shells, uniplicate shell; interareas low, weakly concave in cross-section, ventral interarea apsacline, dorsal interarea anacline; radial ornament costate; lateral margins of ventral sulcus and dorsal fold not covered by costae; fine hollow spines of high density covering the entire shell surface except interareas; ventral interior with teeth supported by long subparallel dental plates to define thickened elongately oval muscle field; cardinalia of two types: with well-developed notothyrial platform or with sessile septalium; cardinal process simple, blade-like; median septum variously developed; dorsal muscle field quadripartite.

Genera assigned. Platystrophia King, 1850; Neoplatystrophia gen. nov.; Vinlandostrophia gen. nov.

Genera questionably assigned. Salacorthis Williams, 1974; Gnamptorhynchos Jin, 1989; Siljanostrophia Zuykov & Egerquist, 2005.

Character	Platystrophia	Neoplatystrophia	Siljanostrophia	Vinlandostrophia	Gnamptorhynchos
Average shell size*	15-20	15-20	15	30–35	15
Diameter of spines*	0.05 - 0.08	0.03-0.06	0.03-0.06	0.03-0.06	0.03-0.06
Density of spines per 1 mm ²	40–60	90–120	90–120	90–120	90–120
Mode of origin of costae in sulcus	Biplicate, uniplicate	Biplicate	Biplicate	Triplicate	Triplicate
Accessory teeth (ventral valve interior)	No	No	No	No	Yes
Septalium	No	Yes	No	Yes	No
Fulcral plates	No	Yes	Yes	Yes	Yes
Notothyrial platform	Yes	No	Yes;	No	Yes;
			free anteriorly		free anteriorly
Median septum between posterior adductors	Yes	No	No	Yes	No
Location of posterior adductors	In valve centre	On flanks	On flanks	In valve centre	On flanks
Posterior adductor scars	Smooth	Smooth; bisected by low ridge	Smooth	With creases	Smooth

Table 1. Morphological comparisons between the genera of Platystrophia-like brachiopods, discussed herein

* Measurements are given in millimetres.

Genera rejected. Mcewanella Foerste, 1920; *Acanthorthis* Neuman, 1976; *Ffynnonia* Neuman & Bates, 1978.

Distribution. Lower Middle Ordovician (Upper Arenig) to the Lower Silurian (Wenlock).

Remarks. This family, as revised here, includes brachiopod genera with a distinctive Spirifer-like shell, costate radial ornament with thin spines, and simple cardinalia. The combination of these morphological features clearly separates this family from all others, which were described in the revised edition of the Treatise (Williams & Harper 2000). However, there are two types of cardinalia, which could suggest that not all taxa within the Platystrophiidae can be accommodated within a single superfamily. The cardinalia of Platystrophia tend to be more similar to those of the Orthoidea (notothyrial platform), whereas those in Neoplatystrophia and Vinlandostrophia are similar to the Plectorthoidea (sessile septalium). A phylogenetic analysis of the platystrophiid brachiopods is required to test this hypothesis, which might imply morphological convergence between these two groups rather than a close phylogenetic relationship.

Gnamptorhynchos and *Siljanostrophia* are similar externally to the genera mentioned above, but on the basis of differences in their cardinalia they are only questionably assigned here. Williams (1974, p. 80) noted differences in the features of the external and internal morphology of *Salacorthis* from *Platystrophia* (*s.l.*). Thus, the assignment of this genus with coarsely costate ornament, a strongly uniplicate anterior margin, and with deep exopuncta (which may be the remains of granulation) to this family remains tentative. Williams & Harper (2000) referred *Mcewanella*, *Acanthorthis*, and *Ffynnonia* to this family, but these undoubtedly plectorthoid genera are quite different from *Platystrophia*-like genera in ornamentation and in the absence of spines.

Genus Platystrophia King, 1850, emend.

Type species. Porambonites costatus Pander, 1830; Obukhovo Formation, Kunda Regional Stage, St Petersburg region, northwest Russia (new designation; see discussion above).

Emended diagnosis. Platystrophiid with uniplicate or biplicate origination of costae in ventral sulcus; dorsal interior with well-developed notothyrial platform; brachiophores with massive basal parts; fulcral plates absent; anterior and posterior pairs of adductor scars closely spaced in the central part of the dorsal valve; median septum well developed, bisecting the adductor scars medially; adductor muscle impressions smooth.

Species assigned. A comprehensive listing is impossible at this point, given that nearly 150 species have been included previously in the genus *Platystrophia* (*s.l.*).

Within our current concept at least 14 taxa belong to the genus *Platystrophia* (s.s.): *P. baltica* sp. nov.; *P. pogrebovi* sp. nov. (see description below); *P. costata* (Pander, 1830); *P. putilovensis* Zuykov, 1999; *P. sublimis* Öpik, 1930; *P. dentata lata* Alichova, 1951; *P. kljasinensis* Zuykov, 1995; *P. dentata trapezoidalis* Alichova, 1951; *P. dentata veimarnensis* Alichova, 1951; *P. crassoplicata* Alichova, 1951; *P. usvaensis* Ivanov in Ivanov & Miagkova, 1950; *P. aff. anomala* Harper & Owen, 1984; *Platystrophia* sp. 2 in Parkes 1994.

Species questionably assigned. P. globularis Andreeva in Andreeva & Misus, 1977 (cardinalia poorly known); ?Platystrophia sp. (Pl. I, fig. 24, herein).

Species rejected. P. chama Eichwald, 1861 (spinose ornamentation unknown); *P. minuta* Benedetto & Herrera, 1987; *P. fasciculata* Benedetto & Herrera, 1987 (reassigned to *Ffynnonia* by Benedetto, 2001, p. 11).

Distribution. Lower Middle Ordovician, Upper Arenig to Upper Ordovician, Upper Caradoc, Estonia, NW Russia, Lithuania, Sweden, Norway, Ireland, (?) UK.

Remarks. The internal features and spinose ornamentation of the majority of *Platystrophia*-like species other than those noted here have not been described or illustrated by previous authors. Therefore the list of the species *Platystrophia* (*s.s.*) as well as those for the two new genera may be subject to considerable revision, when new data on the morphology of other taxa, previously assigned to *Platystrophia* (*s.l.*) are available. For instance, the generic affiliation of *Platystrophia*-like taxa from Wales and China needs careful re-evaluation.

According to Pander (1830, p. 96, pl. XI, fig. 4), "Porambonites dentata n. sp. Feiner gerippt. In der breiteren Bucht zwei Längsrippen." This description of the species from the St Petersburg region (no precise information on the stratigraphic range was reported) was supported by very schematic illustrations. In subsequent publications, however, the name *Platystrophia dentata* was attributed to a wide range of shells with two costae in the sulcus and three on the fold, occurring in Baltoscandia from the Arenig (Ordovician) to the Wenlock (Silurian). Alikhova (1951), Oraspõld (1956), and Bondarev (1968) used the mode of costation for the description of seven subspecies of *P. dentata*, as *veimarnensis*, *lata*, *trapezoidalis*, *triata*, *dentatoides*, *evari*, and *trigonalis*. On the basis of new material we confirm the status of the first four taxa which are assigned here (as separate species) to the genera *Platystrophia* and *Neoplatystrophia*. The status of the other so-called *dentata* forms requires further systematic study.

> *Platystrophia costata* (Pander, 1830) Plate I, figures 1–6; Table 2

- 1830 *Porambonites costatus* n. sp.; Pander, p. 96, pl. XI, fig. 3.
- 1999 *Platystrophia costata* (Pander); Zuykov, p. 200, pl. I, figs 1–14, fig. 4, table 1 (full synonymy).

Neotype. Selected by Zuykov (1999, p. 200), MMI 1/373, Pl. I, figs 1–3, complete shell from the C. H. Pander collection, Pulkovka River, St Petersburg region, NW Russia. Although the type horizon was not originally specified, most probably Pander's specimen is from the so-called lower oolite beds of the Obukhovo Formation, Kunda Regional Stage (*Eoplacognathus variabilis* conodont Biozone).

Material and distribution. 35 complete shells, 9 ventral and 8 dorsal valves; Lower Middle Ordovician (Upper Arenig), Kunda Stage, North Estonia and NW Russia (St Petersburg region).

Diagnosis. Small *Platystrophia* species; subrectangular in outline; ventral sulcus and dorsal fold narrow; radial ornament with one costa in sulcus, two costae on fold, five to six costae on flanks; brachiophores massive, subrhomboidal in cross-section; cardinal process extended anteriorly to join median septum that continues to midvalve.

Remarks. This species occurs commonly in the socalled lower oolite beds of the Obukhovo Formation, Kunda Regional Stage (*Eoplacognathus variabilis* Zone)

Table 2. Measurements (in mm) of *Platystrophia costata*. L = maximum length, W = width, T = thickness, WS = width of the sulcus at the anterior margin, NCS, NCF, NCFV = number of costae in the sulcus and on the fold, and on the flanks of valves

Specimen	L	W	Т	WS	NCS	NCF	NCFV
Neotype, complete shell, MMI 1/373	9.1	10	8.9	_	1	2	5–6
Complete shell, CNIGR 1/12974	7.4	8.9	6	3.4	1	2	5–6
Ventral valve, CNIGR 2/12974	10.6	13	_	5	1	_	6
Complete shell, CNIRG 4/12974	9	10.1	9.9	4.4	1	2	5-6
Complete shell, CNIGR 6/12974	10	14.5	10.2	5.3	3	4	7

of the St Petersburg region. Zuykov (1999) has provided a detailed redescription and discussion of this species. We reillustrate the neotype and some other material.

> *Platystrophia baltica* sp. nov. Plate I, figures 7–13; Figure 2E; Table 3

- non 1820 Terebratulites biforatus n. sp.; Schlotheim, p. 265.
 - 1845 Spirifer biforatus (Schlotheim, 1820); Verneuil, p. 135 (pars).
 - 1890 Platystrophia biforata (Schlotheim); Gagel, p. 35, pl. III, fig. 1, non pl. III, figs 2, 3.
 - 1930 *Platystrophia biforata* (Schlotheim); Öpik, p. 103, pl. V, figs 47–49.
 - 1969 Platystrophia biforata (Schlotheim); Alikhova, p. 17, pl. I, figs 1–3.

Derivation of name. After its geographic distribution in the Baltoscandian Basin.

Holotype. CNIGR 1/13122, Pl. I, figs 7–11, complete shell, northwestern Russia, St Petersburg region, Alekseevka Quarry, Viivikonna Formation, Kukruse Stage, lowermost Upper Ordovician (lower Caradoc).

Material and distribution. Eight complete shells, one ventral and two dorsal valves; Lower Upper Ordovician (Lower Caradoc), Lasnamägi and Uhaku stages of North Estonia; Lasnamägi, Uhaku, and Kukruse stages of the St Petersburg region and the Kukruse Stage of the northwestern part of the Moscow basin, Russia; Uhaku and Kukruse stages of Lithuania. These paratype specimens are reposited in the Central Scientific-Research Geological Exploration Museum, St Petersburg (CNIGR).

Diagnosis. Large *Platystrophia* species with swollen flanks; subrectangular in outline; radial ornament of angular costate; ventral sulcus wide, shallow, with five to seven costae; dorsal fold low, with six to eight costae.

Description. Shell strongly and subequally biconvex with swollen flanks, subrectangular in outline, about 80% as long as wide, with maximum width in anterior third of shell length, 10% as thick as long; cardinal

extremities straight or moderately obtuse. Ventral valve evenly convex in lateral profile, with maximum thickness near mid-length. Ventral sulcus wide, shallow, with steep lateral slopes, originating in umbonal area. Dorsal valve strongly convex. Median fold low, with steep lateral slopes, originating near beak. Five costae in ventral sulcus, six on fold, nine to eleven on flanks of both valves in about 70% of the total individuals; 30% of shells with six to seven costae in sulcus and seven to eight on fold, respectively. Origin of costae in sulcus and on fold, biplicate type of Cumings (1903). Spines with diameter about 0.06 mm and density about 60 per mm².

Brachiophores short, with sharp tips and with moderately stout basal parts, convergent onto anterior of notothyrial platform. Sockets shallow. Adductor scars weakly impressed, bisected by a strong, rounded median ridge, which extends as far forward as the muscle field.

Remarks. Among the specimens assigned to *P. baltica* sp. nov., two groups of individuals can be recognized: those with transverse shells (85% of individuals) (Pl. I, figs 7–11), and specimens with longitudinally elongate shells (15% of individuals), illustrated here on Plate I, figs 12, 13 and in Öpik (1930, pl. V, fig. 48).

Discussion. This species was identified previously as "Platystrophia biforata (Schlotheim, 1820)". Nomenclatorial confusion accompanying this synonymy was introduced by Buch (1837, p. 44) when he suggested (incorrectly) that Schlotheim's specimen (similar externally to Buch's material) was probably from the North (i.e. the Baltic region): "welches wahrscheinlich ebenfalls ein nordisches Stück ist, und nicht aus Frankreich". An extensive search for Schlotheim's original specimen of Terebratulites biforatus in 2002, in the Museum of Natural History, Humboldt University (Berlin), from where it was cited previously in the literature (e.g. Buch 1837, p. 44; Dietrich 1922, p. 124), was unsuccessful. Duplicate casts or labels related to this specimen are also lacking. However, without Schlotheim's original specimen the problem of its generic status cannot be resolved, and "T. biforatus Schlotheim, 1820" must be considered a nomen dubium.

Table 3. Measurements (in mm) of Platystrophia baltica. For abbreviations see Table 2

Specimen	L	W	Т	WS	NCS	NCF	NCFV
Holotype, complete shell, CNIGR 1/13122	21.3	27.5	21.1	14.7	5	6	10
Complete shell, CNIGR 2/13122	23.2	25.8	20.2	17.1	7	8	10
Complete shell, CNIGR 3/13122	19	23.2	18.5	8.5	5	6	10
Ventral valve, CNIGR 4/13122	19+	26	_	_	6	-	11
Dorsal valve, CNIGR 5/13122	13.5+	17.5 +	_	_	_	6	_
Complete shell, CNIGR 6/13122	18	22.8	15.3	13.3	5	6	9

Öpik (1930, p. 100), recognized the existence of two different concepts of *T. biforatus* (Schlotheim 1820, *versus* Buch 1837), but for practical reasons Öpik chose to follow Buch's concept when he described and figured specimens (similar to the specimen described by Schlotheim in the number of costae on different parts of the shell) from the Kukruse Stage of Estonia as "*P. biforata* (Schlotheim)".

> *Platystrophia pogrebovi* sp. nov. Plate I, figures 14–21; Table 4

- non 1830 Terebratula lynx n. sp.; Eichwald, p. 202.
 - 1837 Spirifer lynx (Eichwald); Buch, p. 44.
 - 1840 Spirifer lynx (Eichwald); Eichwald, p. 32 (pars).
 - 1845 *Spirifer lynx* Eichwald; Verneuil, p. 136, pl. III, fig. 4a *non* 3a,b; ?4b.
 - 1861 Platystrophia lynx Eichwald; Eichwald, p. 232.
 - 1884 *Platystrophia lynx* Eichwald; Kiesow, p. 45, pl. II, fig. 13.
 - 1890 Platystrophia biforata var. lynx Eichwald; Gagel, p. 36, pl. III, fig. 3a-c non 3d.
 - 1951 *Platystrophia lynx* Eichwald; Alikhova, p. 16, pl. I, figs 10, 11.
 - 1953 *Platystrophia lynx lynx* Eichwald; Alikhova, p. 25, pl. I, figs 6–8.
 - 1954 *Platystrophia lynx lynx* Eichwald; Alikhova et al., p. 22, pl. XII, figs 1–4.
 - 1969 Platystrophia lynx lynx Eichwald; Alikhova, p. 19, pl. I, figs 4–6.

Derivation of name. In memory of the late Boris S. Pogrebov, photographer in the Department of Paleontology, St Petersburg State University, Russia.

Holotype. CNIGR 5/13126, Pl. I, figs 14–17, complete shell, Kahula Formation, Jõhvi Stage, lowermost Upper Ordovician (lower Caradoc), Aluvere quarry, North Estonia.

Material and distribution. About 400 specimens; Upper Ordovician (Caradoc), Idavere, Jõhvi, and Keila stages of North Estonia and NW Russia (St Petersburg region, Pskov region, Novgorod region), Lithuania; Kullsberg Limestone, Siljan district, Dalarna, Sweden. The paratype specimens are reposited in the Central Scientific-Research Geological Exploration Museum, St Petersburg (CNIGR).

Diagnosis. Large *Platystrophia* species with swollen flanks; subrectangular or trapezoidal in outline; ventral sulcus wide and deep, with three costae; dorsal fold high, with four costae.

Description. Shell strongly and subequally biconvex with swollen flanks, subrectangular or trapezoidal in outline, about 80% as long as wide, with maximum width in anterior third of shell length, 85% as thick as long; cardinal extremities right-angled or obtuse. Ventral sulcus wide, deep, with steep lateral slopes, originating near beak. Dorsal median fold moderately high, originating near beak.

Radial costae high, thin. Three costae in the ventral sulcus, four on the fold, 8–12 on flanks of both valves. Origin of costae in sulcus and on fold of biplicate type of Cumings (1903). Spines with diameter about 0.06 mm and density about 60 per mm². Ornament of concentric growth lamellae, commonly well-preserved.

Umbonal areas strengthened by secondary shell thickening. Some specimens also have a thickening on anterior part of the ventral muscle field (Pl. I, fig. 20). Ovarial impressions in both valves as small pits, usually clearly visible along lateral edges of muscle field. Cardinal process high, bladelike. Brachiophores tusklike, with stout basal parts. Sockets shallow. Adductor scars strongly impressed, bisected by high, rounded median ridge, which extends forward to anterior of muscle field.

Remarks. This species was identified previously as "*Platystrophia lynx lynx* (Eichwald, 1830)". *Terebratula lynx* Eichwald (1830) cannot, however, be identified at present, firstly because of its schematic description and absence of illustrations; secondly, the broad concept of this species used by Eichwald in subsequent papers (1840, 1861); and thirdly, the poorly defined locality and age data, originally given as erratic boulders of Grodno (Republic of Belarus); and finally, the absence of original material in Eichwald's collections. Thus, comparison

Table 4. Measurements (in mm) of Platystrophia pogrebovi. For abbreviations see Table 2

Specimen	L	W	Т	WS	NCS	NCF	NCFV
Holotype, complete shell, CNIGR 5/13126	20.3	22.7	17.7	10.6	3	4	12
Complete shell, CNIGR 1/13126	26.9	29.8	21.8	14.1	3	4	12
Complete shell, CNIGR 6/13126	20.4	23.7	17.5	11.9	3	4	8–9
Complete shell, CNIGR 7/13126	22.7	26.3	19.3	12	3	4	10
Complete shell, CNIGR 8/13126	12.5	22.4	16.7	10.8	3	4	11-12
Dorsal valve, CNIGR 9/13042	18	23.6	17.3	_	3	4	-

between *Terebratula lynx* and other brachiopod species is currently not possible.

Buch (1837, p. 44) redescribed Eichwald's species as *Spirifer lynx* (Eichwald), from a specimen which was also found in erratic boulders from Grodno. This shell is very similar externally to *Platystrophia pogrebovi* sp. nov. Although Eichwald (1840, p. 32) noted that Buch correctly synonymized *Terebratula lynx* with *S. lynx* (Eichwald), he also pointed out that his species can be distinguished from Buch's specimens by the numbers of costae in the sulcus and on the fold. Because the number of costae is a stable feature for this species, Alikhova (1951, p. 17) assumed that these two taxa were most probably not conspecific. We agree with Alikhova, and thus "*Terebratula lynx* Eichwald, 1830" must be also considered a *nomen dubium*.

Here, the new specific name *P. pogrebovi* sp. nov. is proposed for one of the most abundant, widely distributed and easily recognizable brachiopod species in the Upper Ordovician (Caradoc) rocks of Baltoscandia. The absence of data on internal morphology and the poorly defined locality and age data for Buch's original specimen, which is housed in Humboldt Museum in Berlin, negate the use of this shell as a holotype. Thus, one of the specimens from the Kahula Formation of North Estonia is selected as the holotype of *P. pogrebovi*.

Discussion. Jaanusson (1982) noted that specimens similar to *P. pogrebovi* also occur in the Caradoc Kullsberg Limestone of Sweden. This assumption was supported by our examination of brachiopod collections which have been collected by various authors from the Siljan district (Pl. I, figs 18, 19). At the same time, assignment of the Lithuanian specimens to this species is based only on the external features (Alikhova in Alikhova et al. 1954) and thus examination of their internal morphology is required. This was also the reason why specimens described by Alikhova (1951) as *Platy-strophia lynx attenuata* have not been assigned here to *P. pogrebovi*.

Platystrophia pogrebovi differs from *P. dentata lata* Alichova (Alikhova 1951, p. 13) in having a greater number of costae in the sulcus and on the fold, a trapezoidal shell outline, strong convexity of the shells, massive basal parts of the brachiophores, and a thin median septum between the posterior adductor scars.

Genus Neoplatystrophia gen. nov.

Derivation of name. Latin *neo*, new and *Platystrophia*, the brachiopod genus.

Type species. Platystrophia lutkevichi Alichova, 1951, Upper Ordovician Hirmuse Formation, Rakvere Stage, St Petersburg region, NW Russia. *Diagnosis*. Platystrophiid genus with costae in ventral sulcus of biplicate type; cardinalia with sessile septalium; fulcral plates present; posterior adductor scars separated by gap; small median septum variously developed only between anterior adductor scars; muscle scars smooth; posterior adductor scars bisected by variously developed ridges.

Species assigned. P. lutkevichi lutkevichi Alichova, 1951; P. lynx ovalis Alichova, 1951; P. quadriplicata Alichova, 1951; P. dentata triata Oraspõld, 1956; P. lutkevichi satura Oraspõld, 1959; P. saxbyensis Oraspõld, 1959; P. humilis Oraspõld, 1959; P. jaaniensis Rubel, 1963.

Species questionably assigned. Platystrophia lutkevichi contemplata Wright, 1964, from the Ashgill of Ireland, from USNM collections (see here on Pl. II, fig. 15); *P. reversata* (Foerste) from the Brassfield Formation (Early Silurian) of Ohio, USA; *Platystrophia* sp. from the Manitoulin Formation (early Silurian) of Ontario, Canada (no spines preserved, but exteriors and interiors are similar to *Neoplatystrophia*). Schuchert provided the two last identifications for nineteen specimens and one specimen, respectively, for material housed in the Peabody Museum.

The cardinalia of eight "biplicate" *Platystrophia*-like species (see Zuykov 2001) from the Upper Ordovician of Ukraine described by Tsegel'nyuk (1976) may be comparable with cardinalia of *Neoplatystrophia*. However, no data on granulation are given in this publication.

Distribution. Upper Ordovician (Upper Caradoc) to the Lower Silurian (Wenlock), NW Russia, Estonia, Sweden, Lithuania, (?) Ukraine, (?) Ireland, (?) USA, (?) Canada.

Remarks. The sessile septalium, well-developed fulcral plates, the distance between the posterior adductor scars and absence of a median septum between the posterior adductor scars of *Neoplatystrophia* distinguish it from *Platystrophia*. Also, there is double the density of spines in the type species of *Neoplatystrophia* by comparison with those given for the type species of *Platystrophia* is similar to *Vinlandostrophia* in its *Spirifer*-like shell, but differs in having initially two costae in the sulcus, and in the disposition of the dorsal adductor scars, which are also characterized by smooth impressions on the floor of the valve.

Neoplatystrophia lutkevichi lutkevichi (Alichova, 1951) Plate II, figures 3–7; Table 5

- 1951 *Platystrophia lutkevichi* n. sp.; Alikhova, p. 23, pl. I, fig. 18.
- 1953 *Platystrophia lutkevichi* Alichova; Alikhova, p. 25, pl. I, figs 9–12.
- 1954 *Platystrophia lutkevichi* Alichova; Alikhova et al., p. 25, pl. XIV, fig. 1.

Holotype. CNIGR 19/8047, Pl. II, fig. 3, ventral valve, Rakvere Stage, Plyussa River, St Petersburg region, NW Russia.

Material and distribution. About 100 specimens; Upper Ordovician (Upper Caradoc), Rakvere Stage of NW Russia (St Petersburg region); Oandu and Rakvere stages of Lithuania; (?) Oandu and Rakvere stages of Estonia (Rõõmusoks 1970).

Diagnosis. Neoplatystrophia species having moderatesized to large shells, subrectangular in outline with maximum width in anterior third of shell; ventral sulcus deep, wide with two costae umbonally, increased by implantation of costa on each side, so on anterior margin number commonly four; dorsal median fold with three costae in young growth stages, normally external costae developed on outer pair, with branching on either side of median costa in later growth stages, resulting with five costae at anterior margin; on each flank about nine costae which may increase to 12 by development, not only of additional costae along the hingeline at later stages of growth, but by implantation of additional costae.

Discussion. Neoplatystrophia lutkevichi differs from *N. lynx ovalis* (Alichova, 1951) and *N. quadriplicata* (Alichova, 1951) in its greater number of costae in the sulcus and on the fold, which originate by bifurcation and implantation during growth.

Oraspõld (1959) and Wright (1964) erected *satura* and *contemplata* on the basis of their similar style of ornamentation, respectively, as subspecies within *Platystrophia lutkevichi*, from the Ashgill of North Estonia and from Ireland. However, data on granulation in these taxa (and cardinalia in case of *satura*) are absent from the original descriptions. Our material allows us to

recognize Oraspõld's subspecies as useful, but the taxon proposed by Wright is in need of reassessment. The main difference between *N. lutkevichi* and *N. lutkevichi* satura is that the radial costae of the latter taxon are thin and low, so their number on the flanks of both valves increases relative to those of *N. lutkevichi*. The specimen figured on Pl. II, fig. 15 shows that the cardinalia of *P. lutkevichi contemplata* Wright is similar to representatives of the genus *Neoplatystrophia* as is clear from Pl. II, fig. 14.

Rõõmusoks (1970) and Paškevičius (1997) have listed this species from the Oandu and Rakvere regional stages of Estonia and Lithuania, respectively. These specimens were not described or illustrated in either publication, whereas Paškevičius's material was restudied by Zuykov in 2006.

> *Neoplatystrophia jaaniensis* (Rubel, 1963) Plate II, figures 9–11; Figure 2F; Table 6

1963 *Platystrophia jaaniensis* n. sp.; Rubel, p. 120, pl. II, figs 13–16 (see synonymy).

Holotype. GIT, No. 128-1 (old number Br 2900), ventral valve, Jaani Formation, Ninase Member, Jaani Stage, Suuriku, Saaremaa Island, Estonia.

Material and distribution. 28 specimens; Jaani Regional Stage, Wenlock, Silurian of Estonia; Visby Formation, Silurian of Gotland, Sweden.

Diagnosis. Neoplatystrophia species having moderatesized shells, subrectangular or subtrapezoidal in outline, with maximum width at hinge line; radial costae high, sharply angular, two costae in sulcus, three on fold and five to six costae on flanks of both valves.

Table 5. Measurements (in mm) of Neoplatystrophia lutkevichi lutkevichi. For abbreviations see Table 2

Specimen	L	W	Т	WS	NCS	NCF	NCFV
Holotype, ventral valve, CNIGR 19/8047	12.8	18	_	8.5	4	_	9
Complete shell, CNIGR 9/13126	18.7	24.1	17.7	10.9	6	7	11
Dorsal valve, CNIGR 10/13126	16.6+	19+	-	7	-	7	11

Specimen	L	W	Т	WS	NCS	NCF	NCFV
Complete shell, CNIGR 11/13126	12	15.5	11.3	7.6	2	3	5
Complete shell, CNIGR 12/13126	9.8	14	9.1	6.4	2	3	6
Dorsal valve, SMNH Br. 115710	12.8	_	_	_	_	3	6
Ventral valve, SMNH Br. 115711	9.3	15.2	-	7.5	2	-	5

Remarks. The originals of Rubel (1963) are housed in the Institute of Geology, Tallinn University of Technology; the palaeontological collections have been renumbered recently (M. Rubel pers. comm. 2004). The holotype of *Neoplatystrophia jaaniensis* (Rubel, 1963) with an original number of Br 2900 is renumbered now as GIT, No. 128-1.

Discussion. Rubel (1963) described and discussed this species in detail. The types are from the Wenlock Jaani Formation of Estonia, where only rare examples of this species occur. *Neoplatystrophia jaaniensis* is nevertheless common in the Visby Formation of Gotland, Sweden, where, however, their morphology has not been a subject of detailed description or discussion. Based on comparative study of the two, particularly concerning their cardinalia, we consider that the specimens from Sweden (some of which are illustrated here on Pl. II, figs 9–11) are indeed conspecific with the type Estonian *N. jaaniensis* from Suuriku cliff.

Genus Vinlandostrophia gen. nov.

Derivation of name. After "Vinland", which is the historical name for the eastern coast of Canada as used during the age of the Vikings.

Type species. Platystrophia ponderosa Foerste, 1909, Upper Ordovician, Maysvillian, Indiana, USA.

Diagnosis. Large platystrophiid genus, with costae in ventral sulcus of triplicate type; cardinalia characterized by septalium; fulcral plates present; anterior and posterior pairs of adductor closely spaced in the central part of the valve, bisected by median septum; muscle impressions of anterior adductor scars smooth, whereas posterior adductor scars with thin and low creases of secondary shell.

Species assigned. P. ponderosa Foerste, 1909; P. cypha (James, 1874); P. acutilirata (Conrad, 1842); P. laticosta (Meek, 1873).

Distribution. Upper Ordovician (Maysvillian and Richmondian) of Ohio, Tennessee, and Kentucky (see Caster et al. 1961; Alberstadt 1979).

Remarks. As currently conceived, this genus is recognized only in Laurentia to which the core North American species, referred previously to *Platystrophia* (*s.l.*), are assigned here. However, as is clear from the literature (e.g. Alberstadt 1979), and from our examination of museum collections, the species differentiation within North American *Platystrophia*-like brachiopods, which was largely based on external characters, is very difficult, and is impossible in most cases. The taxonomic difficulties that arise from such a situation can be

illustrated by the following example (Alberstadt 1979, p. 14): "The entire range of forms normally referred to by most workers as either *Platystrophia laticosta*, *P. unicostata*, or *P. cypha* comprises a highly variable group having numerous intermediates that are sometimes difficult to identify with any degree of confidence", and "I interpret *P. unicostata* to be synonymous with *P. laticosta*. This interpretation is made because *P. laticosta* and *P. unicostata* are more similar in outline and profile and have approximately the same numbers of plications in the sulcus, on the fold, and on the flanks." It is important to note that in the case of most North American *Platystrophia*-like brachiopods there are no data on their interiors.

In the course of our examination of numerous specimens from the Upper Ordovician (Cincinnatian) of North America, which can be assigned to several groups on the basis of their exteriors, we can infer the similarities between their internal features, in contrast to those of Platystrophia (s.s.). According to Alberstadt (1979), taxonomically, they can most probably be assigned to Platystrophia cypha, P. laticosta, P. acutilirata, and P. ponderosa (Pl. II, figs 17-20; Pl. III, figs 1-4, 7). The last species can also been distinguished from the three others internally because of its distinctive V-shaped sessile septalium (Fig. 2B; Pl. II, figs 19, 20). It seems, therefore, that this character, together with the large size of the shell is useful for the definition of P. ponderosa even if only broken fragments are available. Accordingly, we have therefore selected *P. ponderosa* as the type species for Vinlandostrophia.

Discussion. The posterior adductor scars with creases of secondary shell distinguish *Vinlandostrophia* from all other *Platystrophia*-like brachiopods discussed in this paper. Details on the morphology of the type species and of all other species assigned here to the genus are given by Alberstadt (1979).

Vinlandostrophia ponderosa (Foerste, 1909) Plate II, figures 17–20; Figure 2A,B; Table 7

- 1909 *Platystrophia ponderosa* n. sp.; Foerste, p. 225; pl. IV, fig. 14.
- 1979 Platystrophia ponderosa Foerste, 1909; Alberstadt, p. 16, pl. I, figs 1–21, pl. II, figs 1–27, pl. IV, figs 16, 18–33 (full synonymy).

Holotype. USNM 78814, Pl. II, figs 17, 18, complete shell, Maysvillian, Upper Ordovician, Indiana, USA.

Material and distribution. 53 specimens; Maysvillian, Upper Ordovician, Ohio, USA.

Diagnosis. Vinlandostrophia species having shells quadrate to subquadrate in outline, with maximum width

Specimen	L	W	Т	WS	NCS	NCF	NCFV
Holotype, complete shell, USNM 78814	33.7	40.9	30.5	21	3	4	8
Complete shell, PMSPU 41-1	20.9	28.2	19.3	12.3	3	4	8–9
Complete shell, PMSPU 41-2	30.1	35.2	28.6	17.8	3	4	9
Complete shell, PMSPU 41-3	27.3	34.3	27.9	16.3	3	4	8

Table 7. Measurements (in mm) of Vinlandostrophia ponderosa. For abbreviations see Table 2

in anterior third of shell; radial ornament of angular costate, three costae in sulcus, four on fold and six to eight costae on flanks of both valves; ventral sulcus and dorsal fold prominent, shallow to moderately deep; septalium V-shaped.

Remarks. This species is the most abundant brachiopod taxon amongst Upper Ordovician shelly faunas in the Cincinnati area; it is also represented by numerous specimens in Upper Ordovician brachiopod collections in museums in North America and Europe.

Alberstadt (1979, p. 17) stated that specimens are easily recognizable because "of their distinctively large size, quadrate outline, and presence of a cruraliumlike structure in the brachial valve." He also noted that the presence of a V-shaped cross-section for the sessile septalium as illustrated in Fig. 2B and Pl. II, fig. 20 (see also discussion above) in some specimens is not obvious. This question also arises with comparison of individuals assigned to this species and illustrated in some publications (e.g. Schuchert & Cooper 1932, pl. XII, figs 25, 27). We investigated this uncertainty with reference to numerous specimens from collections in the USGS. We conclude that this is due to the different preservation modes of the studied specimens. Specimens showing a strong degree of shell dissolution of the dorsal internal surface (interiors of such valves are sharply crenulated and adductor scars are invisible) are characterized by a clearly visible V-shaped sessile septalium (Pl. II, fig. 20). Whereas in specimens (both old and young individuals) showing low amounts of shell dissolution, the features of the cardinalia are covered by additional secondary shell (Pl. II, fig. 19) and thus are less visible. However, in another species of Vinlandostrophia, the U-shaped form in the cross-section of the sessile septalium is clearly recognizable (Fig. 2G; Pl. III, fig. 2).

ACKNOWLEDGEMENTS

We thank L. Popov (NMW), S. Long, and R. Cocks (NHM, London) for their help with the study of Thomas Davidson's collections and helpful comments; M. Aberhan (NHM, Berlin), J. Bergström (SMNH), S. Butts (Peabody Museum), T. Dutro and R. Neuman (Smithsonian Institution), A. Miller (University of Cincinnati), and J. Paškevičius (Vilnius University) for access to brachiopod collections. F. Alvarez (University of Oviedo), J. Jin (University of Western Ontario), M. Rubel (University of Tartu), Y. V. Savitskiy (St Petersburg State University), and A. D. Wright (University of Leicester) are thanked for helpful discussions and critical comments on the manuscript. Important specimens were donated to the authors by T. N. Alikhova, L. Hints, H. Leipnitz, V. A. Nasedkina, J. L. Benedetto, P. V. Fedorov, L. Popov, S. S. Terentiev, R. Fine, and J. Tate. M.Z. specially thanks M. G. Bassett (NMW) for his critical comments, and help during his visits to NMW. Different stages of this work by M.Z. have been supported by grants from the Sylvester-Bradley Award (Palaeontological Association), Association of Applied Paleontological Sciences, Paleontological Society, Dry Dredgers Paul Sanders Award (USA), Smithsonian Institution (Washington DC), Theodore Roosevelt memorial grant and Collection Study Grant (AMNH), Ernst Mayr Grant (Harvard University, USA), and C. Schuchert and A. Dunbar Grant (Yale University, USA). D.A.T.H. thanks the Carlsberg Foundation (Denmark) for financial support. Photographs were taken by S. Butts, E. Egerquist, B. S. Pogrebov, P. V. Stepanov, and M. A. Zuykov. The final manuscript benefited considerably from thorough and helpful reviews by Fernando Alvarez and Michael Bassett. This paper is a contribution to IGCP Project 503.

REFERENCES

- Alberstadt, L. P. 1973. Articulate brachiopods of the Viola Formation (Ordovician) in the Arbuckle Mountains, Oklahoma. Oklahoma Geological Survey Bulletin, 117, 1–90.
- Alberstadt, L. P. 1979. The Brachiopod genus *Platystrophia*. United States Geological Survey, Professional Papers, 1066-B, 1–20.
- Alexander, R. R. 2001. Functional morphology and biomechanics of articulate brachiopod shells. In *Brachiopods Ancient and Modern* (Carlson, S. J. & Sandy, M. R., eds), *The Paleontological Society Papers*, 7, 145–169.

- Alikhova, T. N. 1951. Brakhiopody srednej i verkhnej chasti nizhnego silura Leningradskoj oblasti i ikh stratigraficheskoe znachenie [Brachiopods of the middle and upper parts of the lower Silurian of Leningrad region and their stratigraphical significance]. Gosgeolizdat, Moscow, 80 pp. [in Russian].
- Alikhova, T. N. 1953. Rukovodyashchaya fauna brakhiopod ordovikskikh otlozhenij severo-zapadnoj chasti Russkoj platformy [Key taxa of the brachiopod fauna of the Ordovician of the northwestern part of the Russian Platform]. Gosgeolizdat, Moscow, 163 pp. [in Russian].
- Alikhova, T. N. 1960. Orthida. In Osnovy paleontologii [Fundamentals of palaeontology] (Sarycheva, T. G., ed.), pp. 183–197. Russian Academy of Sciences, Moscow [in Russian].
- Alikhova, T. N. 1969. Stratigrafiya i brakhiopody sredneordovikskikh otlozhenij Moskovskoj sineklizy [Stratigraphy and brachiopods of the Middle Ordovician deposits of the Moscow Syneclise]. Nedra, Moscow, 91 pp. [in Russian].
- Alikhova, T. N., Balashova, E. A. & Balashov, Z. G. 1954. Polevoj atlas kharakternykh kompleksov fauny otlozhenij ordovika i gotlandiya yuzhnoj chasti Litovskoj SSR [Field atlas of characteristic Ordovician and Gotlandian faunal associations of the southern part of the Lithuanian SSR]. Gosgeolizdat, Moscow, 100 pp. [in Russian].
- Alvarez, F. & Brime, C. 2000. Type specimens of athyridid brachiopods from the James Hall Collection. *The Uni*versity of Kansas, Paleontological Contributions, New Series, 12, 1–15.
- Alvarez, F. & Carlson, S. J. 1998. Evolution and phylogenetic relationships among athyridide higher taxa and other "articulate brachiopods". *Revista Española de Paleontología*, 13, 209–234.
- Alvarez, F. & Rong Jia-yu, 2002. Athyridida. In *Treatise on Invertebrate Paleontology*, Vol. 4 (Kaesler, R. L., ed.), pp. H1475–H1601. Geological Society of America and University of Kansas Press, Boulder and Lawrence.
- Alvarez, F. & Taylor, P. D. 1987. Epizoan ecology and interactions in the Devonian of Spain. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, **61**, 1–2, 17–31.
- Andreeva, O. N. & Misus, P. P. 1977. The new orthids from the Middle Ordovician of Tian'-Shan' and Pre-Polar Ural. In Novye vidy drevnikh rastenij i bespozvonochnykh SSSR. Chast' 4 [New species of fossil plants and invertebrates of the USSR, part 4] (Abushik, A. F. & Grygorieva, A. D., eds), pp. 106–110. Nauka, Moscow [in Russian].
- Bassett, M. G. 1972. The articulate brachiopods from the Wenlock Series of the Welsh Borderland and South Wales. Part 2. *Palaeontographical Society (London)*, *Monograph*, **126**, 532, 27–78.
- Bassett, M. G., Cocks, L. R. M., Holland, C. H., Rickards, R. B.
 & Warren, P. T. 1975. The type Wenlock Series. *Report* of the Institute of Geological Sciences, 75/13, 1–19.

- Bather, F. A. 1920. A study of the Brachiopod genus *Platystrophia* by Eula Davis McEwan. Review. *Geological Magazine*, 57, 88–90.
- Benedetto, J. L. 2001. Silicified early Ordovician (Arenig) brachiopods from the San Juan Limestone (Argentine Precordillera). *Geologica et Palaeontologica*, 35, 1–29.
- Benedetto, J. L. & Herrera, Z. A. 1987. The genus *Platystrophia* King (Brachiopoda) in the San Juan Formation of the Argentinian Precordillera. *Ameghiniana*, 24, 51–59.
- Bondarev, V. I. 1968. Stratigraphy and characteristic brachiopods of the Ordovician deposits of southern Novaya Zemlya, Vaigach Island and northern Paj-Khoy. In Stratigrafiya, usloviya osadkonakopleniya i fauna ordovikskikh i nizhnedevonskikh otlozhenij Novoj Zemli, Vajgacha i Paj-Khoya [Stratigraphy, sedimentary conditions and fauna of the Ordovician and Lower Devonian deposits of Novaya Zemlya, Vaigach Island and Paj-Khoy] (Bondarev, V. I., ed.), pp. 3–144. Nedra, Leningrad [in Russian].
- Brunton, C. H. C., Alvarez, F. & MacKinnon, D. I. 1996. Morphological terms used to describe the cardinalia of articulate brachiopods: homologies and recommendations. *Historical Biology*, **11**, 9–41.
- Buch, L. 1837. *Über Delthyris oder* Spirifer *und* Orthis. Berlin, 80 pp.
- Caster, K. E., Dalve, E. A. & Pope, J. K. 1961. Elementary Guide to the Fossils and Strata of the Ordovician in the Vicinity of Cincinnati, Ohio. Cincinnati Museum of Natural History, Ohio, 47 pp.
- Cocks, L. R. M. 1978. A review of British Lower Palaeozoic brachiopods, including a synoptic revision of Davidson's Monograph. *Palaeontographical Society (London), Mono*graph, 131 (549), 1–256.
- Conrad, T. A. 1842. Observations on the Silurian and Devonian systems of the United States with descriptions of new organic remains. *Academy of Natural Sciences of Philadelphia, Journal*, 8, 2, 228–280.
- Cumings, E. R. 1903. The morphogenesis of *Platystrophia*. A study of the evolution of a Paleozoic brachiopod. *American Journal of Science, Series 4*, **15**, 85, 1–48.
- Davidson, T. 1848. Memoire sur les brachiopodes du system superieur d'Angleterre. Société Géologique de France, Bulletin, Series 2, 5, 309–338.
- Davidson, T. 1871. A monograph of the British fossil Brachiopoda (Vol. 3, Part 7. No 4: Silurian Brachiopoda). *Palaeontographical Society (London), Monograph*, 24, 249–397.
- Dietrich, W. O. 1922. Bemerkung zum Genotype der Brachiopodengattung *Platystrophia. Zentralblatt für Mineralogie, Geologie und Palaeontologie*, 123–124.
- Eichwald, E. 1830. Naturhistorische Skizze von Lithauen, Volhynien und Podolien. Wilna, 256 pp.
- Eichwald, E. 1840. Ueber das silurische Schichtensystem in Esthland. St. Petersburg, 243 pp. [in Russian].

- Eichwald, E. 1861. *Paleontologiya Rossii. Drevnij period, 2* [*Palaeontology of Russia. Ancient period, 2*]. St. Petersburg, 521 pp. [in Russian].
- Erlanger, O. A. 1994. The Devonian rhynchonellids of Mongolia. Sovmestnaya Rossiisko–Mongol'skaya Paleontologicheskaya Ekspeditsiya, Trudy, 45, 1–144 [in Russian].
- Fitzpatrick, K. T. 1971. The shell structure and micro-ornament of *Platystrophia*, an orthid brachiopod. *The Compass* (of Sigma Gamma Epsilon), **49**, 29–38.
- Foerste, A. F. 1909. Preliminary notes on Cincinnatian fossils. Denison University, Scientific Laboratories, Bulletin, 14, 208–231.
- Foerste, A. F. 1920. The Kimmswick and Plattin limestones of northern Missouri. *Denison University, Scientific Laboratories, Bulletin*, **19**, 175–224.
- Gagel, C. 1890. Die Brachiopoden der cambrischen und silurischen Geschiebe im Diluvium der Provinzen Ostund Westpreussen. *Beiträge zur Naturkunde Preussens*, 6, 1–79.
- Grunt, T. A. 1989. Otryad Athyridida (evolyutsionnaya morfologiya i istoricheskoe razvitie) [Order Athyridida (evolutionary morphology and phylogeny)]. Nauka, Moscow, 142 pp. [in Russian].
- Hall, J. & Clarke, J. M. 1892. An introduction to the study of the genera of Palaeozoic Brachiopoda. *New York Geological Survey, Paleontology*, 8, 1, 1–367.
- Hall, J. & Clarke, J. M. 1893. An introduction to the study of the genera of Palaeozoic Brachiopoda. *New York Geological Survey, Paleontology*, 8, 2, 1–317.
- Harper, D. A. T. & Owen, A. W. 1984. The Caradoc brachiopod and trilobite fauna of the upper Kirkerud Group, Hadeland, Norway. *Geologica et Palaeontologica*, 18, 21–51.
- [ICZN] International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature, 4th Edition. International Trust of Zoological Nomenclature, London, xxix + 306 pp.
- Ivanov, A. N. & Miagkova, E. I. 1950. Ordovician fauna of the western slope of the Central Urals. Akademiya Nauk SSSR, Ural'skij filial, Gorno-Geologicheskij Institut (Sverdlovsk), 18, 1–32 [in Russian].
- Jaanusson, V. 1982. The Siljan district. In Field Excursion Guide. Fourth International Symposium on the Ordovician System (Bruton, D. L. & Williams, S. H., eds), Paleontological Contributions, University of Oslo, 279, 15–42.
- James, U. P. 1874. Description of new species of brachiopods from the lower Silurian rocks of the Cincinnati Group. *Cincinnati Quarterly Journal of Science*, **1**, 19–22.
- Jin Jisuo. 1989. Late Ordovician–Early Silurian rhynchonellid brachiopods from Anticosti Island, Québec. *Biostrati*graphie du Paléozoique, 10, 1–127.
- Jin Jisuo & Zhan Renbin. 2000. Evolution of the late Ordovician orthid brachiopod *Gnamptorhynchos* Jin, 1989

from *Platystrophia* King, 1850, in North America. *Journal* of *Paleontology*, **74**, 983–991.

- King, W. 1850. A monograph of the Permian Fossils of England. Palaeontographical Society (London), Monograph, 3, 1, 1–258.
- Kiesow, J. 1884. Ueber silurische und devonische Geschiebe Westpreussens. Schriften der Naturforschenden Gesellschaft zu Danzig, Neue Folge, 16, 205–300.
- Lazarev, S. S. 1976. Morphology and evolution of brachiopods (of the superfamily Enteletacea). Akademiya Nauk SSSR, Paleontologicheskij Institut, Trudy, 154, 1–167 [in Russian].
- M'Coy, F. 1846. A Synopsis of the Silurian Fossils of Ireland Collected from the Several Districts by Richard Griffith F.G.S. Dublin, 72 pp.
- Meek, F. B. 1873. Description of the invertebrate fossils of the Silurian and Devonian systems. *Geological Survey of Ohio, Report*, 1, 2, 1–243.
- Neuman, R. B. 1976. Early Ordovician (Late Arenig) brachiopods from Virgin Arm, New World Island, Newfoundland. *Geological Survey of Canada, Bulletin*, 261, 11–61.
- Neuman, R. B. & Bates, D. E. B. 1978. Reassessment of Arenig and Llanvirn age (Early Ordovician) brachiopods from Anglesey, North-West Wales. *Palaeontology*, 21, 571–613.
- Nõlvak, J. 1997. Ordovician. Introduction. In Geology and Mineral Resources of Estonia (Raukas, A. & Teedumäe, A., eds), pp. 52, 54–55. Estonian Academy Publishers, Tallinn.
- Öpik, A. 1930. Brachiopoda Protremata der Estlandischen Ordovizischen Kukruse-Stufe. *Acta et Commentationes Universitatis Tartuensis*, A XVII, 1–262.
- Oraspõld, A. L. 1956. New brachiopods of the Jõhvi, Keila and Vasalemma stages. *Eesti NSV Teaduste Akadeemia Geoloogia Instituudi Uurimused*, 1, 41–67 [in Russian].
- Oraspõld, A. L. 1959. Some representatives of the superfamily Orthacea from the upper Ordovician of Estonia. *Tartu* Ülikooli Geoloogia Instituudi Toimetised, 75, 51–81 [in Russian].
- Pander, C. H. 1830. *Beiträge zur Geognosie des Russischen Reiches*. St.-Petersburg, 165 pp.
- Parkes, M. A. 1994. The brachiopods of the Duncannon Group (Middle–Upper Ordovician) of southeast Ireland. *British Museum (Natural History), Bulletin (Geology)*, **50**, 105– 174.
- Paškevičius, J. 1997. *The Geology of the Baltic Republics*. Vilnius University and Geological Survey of Lithuania, Vilnius, 387 pp.
- Rõõmusoks, A. 1970. Stratigrafiya viruskoj i har'yuskoj serij (ordovic) Severnoj Éstonii [Stratigraphy of the Viru and Harju Series (Ordovician) of North Estonia]. Valgus, Tallinn, 346 pp. [in Russian, with English summary].
- Rubel, M. P. 1963. Silurian brachiopods Orthida of Estonia. *Eesti NSV Teaduste Akadeemia Geoloogia Instituudi Uurimused*, 13, 109–160 [in Russian, with English summary].

- Sartenaer, P. 1969. Late Upper Devonian (Famennian) rhynchonellid brachiopods from western Canada. Geological Survey of Canada, Bulletin, 169, 1–269.
- Sartenaer, P. 1970. Nouveaux genres rhynchonellides (brachiopodes) du Paleozoique. *Institut Royal des Sciences Naturelles de Belgique, Bulletin*, **46**, 1–32.
- Savage, N. M., Mancenido, M. O., Owen, E. F., Carlson, S. J., Grant, R. E., Dagys, A. S. & Sun Dong-Li. 2002. Rhynchonellida. In *Treatise on Invertebrate Paleontology, Part H, Revised, Brachiopoda, Vol. 4* (Kaesler, R. L., ed.), pp. 1027–1376. Geological Society of America and University of Kansas Press, Boulder and Lawrence.
- Schlotheim, E. F., von. 1820. Die Petrefactenkunde auf ihrem jetzigen Strandpunkte durch die Beschreibung einer Sammlung versteinerter und fossiler Uberreste des Tierund Pflanzenreichs der Vorwelt erlautert, Vol. 1. Gotha, 437 pp.
- Schuchert, C. 1897. A synopsis of American fossil Brachiopoda, including bibliography and synonymy. United States Geological Survey, Bulletin, 87, 1–464.
- Schuchert, C. & Cooper, G. A. 1932. Brachiopod genera of the suborders Orthoidea and Pentameroidea. *Peabody Museum of Natural History, Memoirs*, 4, 1, 1–270.
- Schuchert, C. & LeVene, C. M. 1929. Brachiopoda (generum et genotyporum index et bibliographia). In *Fossilium Catalogus, Vol. 1, Animalia, Pars 42* (Pompeckj, J. F., ed.), pp. 1–140. W. Junk, Berlin.
- Sinclair, G. W. 1946. Some species of *Platystrophia* from the Trenton of Ontario and Quebec. *Paleontographica Americana*, **3**, 271–284.
- Tsegel'nyuk, P. D. 1976. Brakhiopody i stratigrafiya nizhnego paleozoya Volyno-Podolii [Lower Palaeozoic brachiopods and stratigraphy of Volyno-Podolia]. Naukova Dumka, Kiev, 156 pp. [in Russian].
- Twenhofel, W. H. 1928. Geology of Anticosti Island. Geological Survey of Canada, Memoir, 154, 1–351.
- Verneuil, E. P. 1845. Paleontologie. In Geologie de la Russie d'Europe et des Montagnes de l'Oural, Vol. 2, pt. 3 (Murchison, R. I., Verneuil, E. P. & Keyserling, A., eds), pp. 246–285. Paris.
- Williams, A. 1962. The Barr and Lower Ardmillan Series (Caradoc) of the Girvan District, South-West Ayrshire, with descriptions of the Brachiopoda. *Geological Society* of London, Memoir, 3, 1–267.
- Williams, A. 1963. The Caradocian brachiopod faunas of the Bala District, Merionethshire. *British Museum (Natural History), Bulletin (Geology)*, 8, 327–471.
- Williams, A. 1974. Ordovician Brachiopoda from the Shelve District, Shropshire. British Museum (Natural History), Bulletin (Geology) Supplement, 11, 1–163.
- Williams, A. & Brunton, C. H. C. 1997. Glossary of morphological and selected anatomical terms. In *Treatise on Invertebrate Paleontology, Part H, Revised, Brachiopoda, Introduction* (Kaesler, R. L., ed.), pp. 423–440. Geological

Society of America and University of Kansas Press, Boulder and Lawrence.

- Williams, A. & Harper, D. A. T. 2000. Orthida. In *Treatise on Invertebrate Paleontology, Part H, Revised, Brachiopoda, Vol. 3* (Kaesler, R. L., ed.), pp. 714–844. Geological Society of America and University of Kansas Press, Boulder and Lawrence.
- Williams, A. & Wright, A. D. 1963. The classification of the "Orthis testudinaria Dalman" group of brachiopods. Journal of Paleontology, 37, 1–32.
- Williams, A. & Wright, A. D. 1965. Order Orthida. In *Treatise* on Invertebrate Paleontology, Part H, Brachiopoda, Vol. 1 (Moore, R. C., ed.), pp. 209–355. Geological Society of America and University of Kansas Press, Boulder and Lawrence.
- Williams, A., Rowell, A. J., Ager, D. V., Elliott, G. F., Grant, R. E., Muir-Wood, H. M. & Stehli, F. G. 1965. Morphological terms applied to brachiopods. In *Treatise* on Invertebrate Paleontology, Part H, Brachiopoda, Vol. 1 (Moore, R. C., ed.), pp. 139–155. Geological Society of America and University of Kansas Press, Boulder and Lawrence.
- Williams, A., Carlson, S. J., Brunton, C. H. C., Holmer, L. E. & Popov, L. E. 1996. A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London (series B)*, 351, 1171–1193.
- Wright, A. D. 1964. The fauna of the Portrane Limestone, II. British Museum (Natural History), Bulletin (Geology), 9, 157–256.
- Wright, A. D. & Rubel, M. 1996. A review of the morphological features affecting the classification of clitambonitidine brachiopods. *Palaeontology*, **39**, 53–75.
- Zuykov, M. A. 1995. New species of brachiopods from the Middle Ordovician of the St. Petersburg region (Orthida, Plectorthidae). *Proceedings of the St. Petersburg State University, Serie 7, Geology*, **3**, 21, 108–111 [in Russian].
- Zuykov, M. A. 1999. Platystrophia (Orthida, Brachiopoda) from the Arenig and lowermost Llanvirn of northwestern Russia. Proceedings of the Estonian Academy of Sciences, Geology, 48, 195–212.
- Zuykov, M. A. 2001. Platystrophia (Orthida) in the Ordovician and Early Silurian of the East Baltic. In Brachiopods: Past and Present (Brunton, C. H. C., Cocks, L. R. M., Long, S. L., eds), pp. 327–334. Systematics Association Special Volume, 63. Taylor & Francis, London and New York.
- Zuykov, M. A. & Egerquist, E. 2005. A new *Platystrophia*like brachiopod genus from the Ordovician Boda limestones of Dalarna, Sweden. *GFF*, **127**, 1–5.
- Zuykov, M. A. & Harper, D. A. T. 2004. Platystrophia King, 1850 (Brachiopoda, Orthida): proposed conservation of usage by designation of *Porambonites costatus* Pander, 1830 (currently *Platystrophia costata*) as the type species of *Platystrophia*. Bulletin of Zoological Nomenclature, 61, 246–250.

Platystrophia (Orthida) ja uued sugulaslikud Ordoviitsiumi ja Vara-Siluri käsijalgsete perekonnad

Mihhail A. Zuikov ja David A. T. Harper

Alles hiljuti oli koja spiriferoidne väliskuju peamiseks kriteeriumiks, mille alusel loeti Ordoviitsiumi ja Siluri käsijalgsed perekonda *Platystrophia* King kuuluvaiks. Traditsiooniliselt käsitleti *Platystrophia* tüüpliigina liiki *Terebratulites biforatus* Schlotheim (1820), mis pärineb ilmselt Prantsusmaa Juurast. Tegelikult püstitas W. King nimetatud perekonna *Orthis biforata* eksemplaride põhjal, mida kirjeldas T. Davidson (1848) Inglismaa Wenlockist (Silur). Rahvusvahelise Zooloogilise Nomenklatuuri Koodeksi (1999) põhjal peetakse Kingi (1850) *Platystrophia biforata* autoriks ja selle liigi (mitte *T. biforatus*) fikseeris ta *Platystrophia* tüüpliigina. Davidsoni eksemplarid ei ole säilinud ja avaldatud kirjeldused ei ole informatiivsed. Autorid on esitanud RZN Komisjonile taotluse määrata uueks tüüpliigiks *Porambonites costatus* Pander (1830). See ettepanek on aktsepteeritud komisjoni seisukohas nr 2154. Täpsustatud diagnoosi alusel kuuluvad perekonda *Platystrophia* (s.s.) liigid, mis esinevad Baltika ja Avalonia Arenigist kuni Ülem-Karadokini, kuid sama piirkonna Ashgilli ja Alam-Siluri vormid (võib-olla ka mõned Laurentia liigid) kuuluvad uude perekonda *Neoplatystrophia*. Liiki *Platystrophia ponderosa* Foerste Põhja-Ameerika Ülem-Ordoviitsiumist käsitletakse kui uue perekonna *Vinlandostrophia* tüüpliiki. Artiklis on esitatud kuue taksoni kirjeldused, sh kõigi uute taksonite käsitlused.