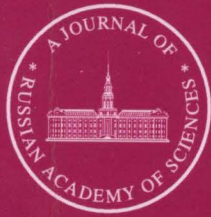


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# **Ordovician Trilobites of the Subfamily Asaphinae of the Ladoga Glint**

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# Contents

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INTRODUCTION	S229
1. STRATIGRAPHY	S229
1.1. <i>Stratigraphic Units of the Carbonate Part of the Ladoga Glint Ordovician</i>	S232
1.2. <i>Trilobite-Based Biostratigraphic Divisions of the Carbonate Ordovician Deposits of the Ladoga Glint</i>	S248
2. PALEONTOLOGY	S256
2.1. <i>The Morphology of Trilobites of the Subfamily Asaphinae</i>	S256
2.2. <i>Some Data on the Ecology of the Asaphinae: Living and Taphonomical Environments</i>	S260
2.3. <i>Evolution of the Subfamily Asaphinae in the Volkhov-Uhakian Time</i>	S263
2.4. <i>Systematic Paleontology of the Subfamily Asaphinae</i>	S265
ACKNOWLEDGMENTS	S334
REFERENCES	S334

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**Abstract**—Trilobites of the subfamily Asaphinae Burmeister (genus *Asaphus* s.l.) coming from natural outcrops of the Ordovician beds on the southern shore of Lake Ladoga are monographically studied and revised. Forty-one taxa of the generic and specific ranks, including seven new taxa, are described; they constitute more than three-quarters of this widely known group of European Ordovician trilobites. Some points of asaphine ecology and phylogeny are considered. Considerable attention is paid to the stratigraphy of the Early–Middle Ordovician deposits of the eastern part of the northern Estonia–Lithuania confacial belt or the gray limestone zone, which is the parental facies of many trilobite groups of the Baltic Paleobasin.

**Key words:** trilobites, Asaphinae, Russia, Ladoga, Ordovician.

## INTRODUCTION

The Ordovician plateau located in northern Estonia and the Leningrad Region represents the easternmost outcrop of the Early Paleozoic deposits of the Baltoscandian paleobasin (Fig. 1a). The northern margin of the plateau is known in the literature as the Baltic–Ladoga Glint. The abundance of natural outcrops and mines in this region facilitates study of the sections, and the diversity and superb preservation of fossils allow an exceptionally comprehensive reconstruction of the organic world of the Ordovician sea.

Since Lamanskii's time, i.e., the last 100 years, the stratigraphy of the carbonate part of the Glint (Volkhov, Kunda, Aseri, Lasnamägi, and Uhaku horizons) has been nearly exclusively based on trilobites of the genus *Asaphus*; however, the diversity of recorded representatives of the subfamily Asaphinae is far from being limited to index species. The facial zone covering the Glint sections was the main area of distribution and, probably, became from time to time a center of diversification. Thus, numerous phases of the origin and evolution of species of this subfamily were recorded in the sections.

The most numerous and diverse finds of asaphines have been made on the southern shore of Lake Ladoga, i.e., within the Ladoga part of the Glint (Fig. 1b). In addition to abundant fossils, not only trilobites, this region is interesting because of the deposits that are distributed both in undersurface strata within the Baltic Region and in deep-seated strata of the Moscow Syncline. Some members, beds, and discontinuity surfaces of these deposits can be traced over tens or even hundreds of kilometers, if the Baltic part of the Glint is taken into account. In the future, this may help in pinpointing the depositional settings and the stratigraphic and lateral succession of organic forms within the area under study.

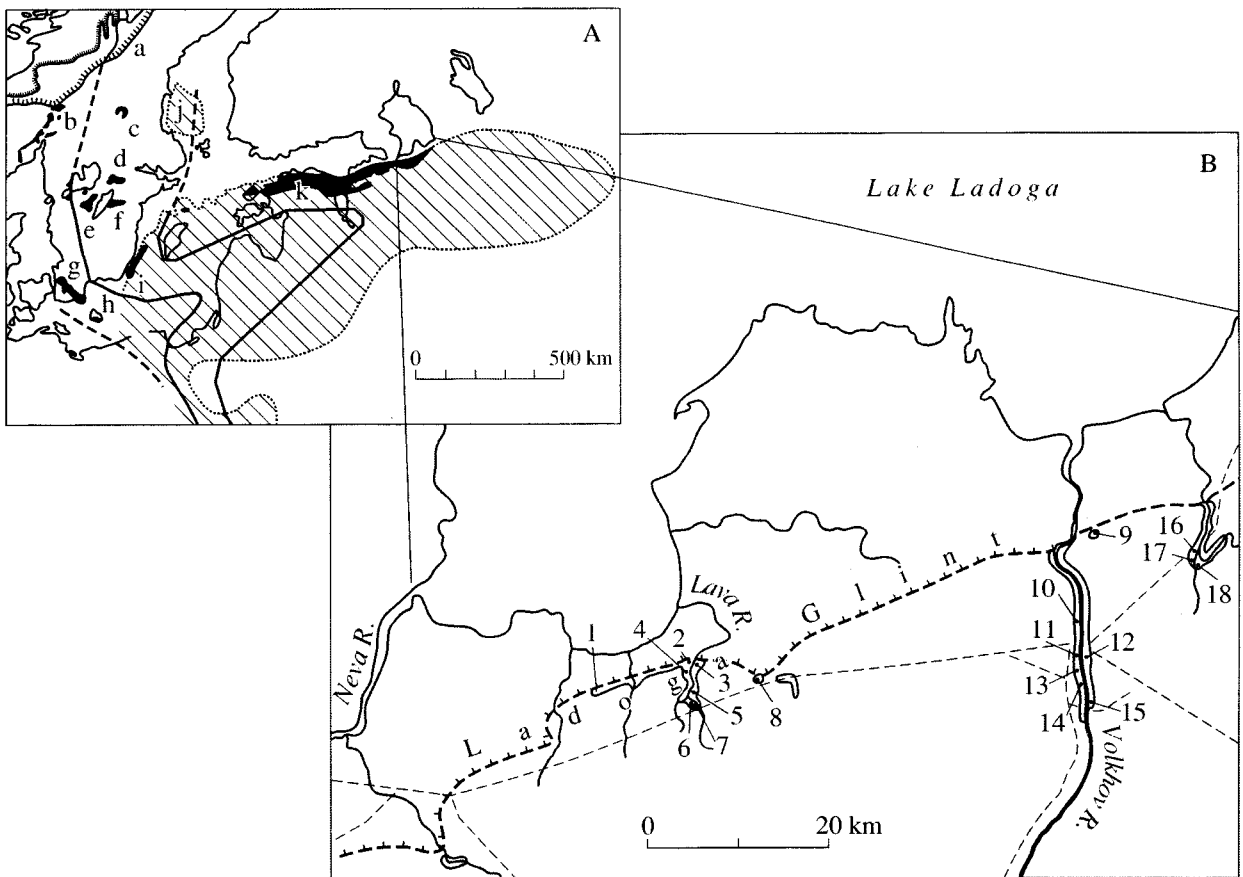
This paper seeks to systematically describe asaphines and clarify their stratigraphic distribution. Newly obtained data led us to revisions in the system of this subfamily and its phylogenetic relationships and to changes in the trilobite scheme of carbonate deposits of the Eastern Baltic Region adopted by the Interdepart-

mental Conference of Stratigraphy of the Ordovician and Silurian of the East European Platform in 1984.

This work is based on the collection of asaphines housed at the Department of Paleontology of St. Petersburg State University, which was gathered by generations of geologists (the names of M.E. Yaroshevskii, A.F. Lesnikova, R.F. Hecker, V. Kotlukov, E.A. Balashova, R.S. Eltyshova, and many other geologists are written on the labels), as well as on my geological observations and my personal collection (PIN, no. 4330). Additionally, I studied the collections stored in the geological museums of the All-Russia Geological Institute (GMAGI); Departments of Paleontology and Historical Geology of the St. Petersburg State University (DPStPSU and DHGStPSU, respectively); St. Petersburg State Mining Institute (StPSMI); Paleontological Institute, Russian Academy of Sciences (PIN); Museum of Nature, Tallinn, Estonia (TMN); Paleontological Museum, Oslo, Norway (PMO); Sweden Museum of Natural History (RM); and the personal collections of F.B. Schmidt (GMAGI, no. 11152, DHGStPSU, no. 149, PIN, no. 4248), V.V. Lamanskii (DHGStPSU, no. 155), E.A. Balashova (DPStPSU, no. 9243), E.I. Eichwald (DHGStPSU, no. 1), R.F. Hecker (StPSMI), C. Boeck, W. Brögger, B. Wandas (PMO), and some others. In addition, I have examined the lectotype of *Asaphus* (*Asaphus*) *expansus*, which is the type species of the type genus of the subfamily; the original specimen by B. Wahlenberg is stored at the Paleontological Institute of the University of Uppsala, Sweden (PIUU).

## 1. STRATIGRAPHY

The geological study of the Baltic–Ladoga Glint started at the border between the 18th and 19th centuries, when I. Georg and V.I. Severigin published their general observations on its structure. During the starting period, which lasted for about a century, preliminary geological data and fossil collections were gathered to show that the Glint deposits belong to the Cambrian and Lower Silurian (Ordovician). According to the historical essays that may be found in Lamanskii



**Fig. 1.** A: Outcrops of Ordovician deposits in the Baltoscandia (solid filling) and their near-surface and underwater distribution (hatched area): (a) Jämtland, (b) Oslo Region, (c) Lake Siljan Region, (d) Narke, (e) Västergötland, (f) Östergötland, (g) Scania, (h) Bornholm Island, (i) Öland Island, (j) Southern Bothnian underwater region, (k) Northern Estonia and Leningrad Region; (I–III) confacial belts: (I) Denmark–Norway Belt, (II) Sweden–Livonia Belt, (III) Northern Estonia–Lithuania Belt (Jaanusson, 1982; Dronov *et al.*, 1998); B: Map of localities studied: (1) Putilovskii Kar'er, (2) Gorodishche, (3) Gorodishchenskii Kar'er, (4) Vasil'kovo, (5) Kavra, (6) North Naziya, (7) South Naziya, (8) Voibokalo, (9) Babino, (10) Zvanka, (11) Volkhov power station dam, (12) Duboviki, (13) Shkurina Gorka, (14) Porogi–Valim, (15) Bor, (16) Lynna Mouth, (17) Khamontovo, (18) Southern Lynna.

(1901), Orviku (1960b), Hecker (1987), Popov *et al.* (1989), A.F. Folbort, Ch.I. Pander, E.I. Eichwald, and S.S. Kutorga were the most renowned paleontologists of that time. This period culminated at the end of the 19th century in the series of Schmidt's papers (1898, 1901, etc.), in which a clear stratigraphic scheme of the Cambrian–Silurian deposits of the Baltic Region was provided and all found trilobites were described. In the limestone of the Glint, Schmidt (Lamanskii, 1901) recognizes stage B with the substages B<sub>2</sub> (glauconite Limestone) and B<sub>3</sub> (vaginate Limestone) and stage C (substage C<sub>1</sub>, *Echinospaerites* Limestone) (Table 1).

Simultaneously with the last volumes of Schmidt's monograph on the East Baltic trilobites, a paper by Lamanskii was published; he recognized horizons with fauna within the deposits of the B stage, published lists of all fossils found, and traced facial changes of rocks along the Glint from the Syas' River on the east to the Baltic Port (Paldiski) on the west. He also proposed the name *Ladoga Glint* for the eastern part of the Glint cor-

responding to the southern part of Lake Ladoga (Lamanskii, 1901). In the limestone of the Ladoga Glint, Lamanskii (1901, 1905) described the following faunistic horizons (sometimes treated by him as zones): B<sub>II</sub><sup>α</sup> with *Asaphus priscus*, *Megalaspis planilimbata*, and *M. limbata*; B<sub>II</sub><sup>β</sup> with *A. broeggeri* and *Onchometopus volborthi*; B<sub>II</sub><sup>γ</sup> with *A. lepidurus* and *M. gibba*; B<sub>III</sub><sup>α</sup> with *A. expansus* and *A. lamanskii*; B<sub>III</sub><sup>β</sup> with *A. raniceps*; and B<sub>III</sub><sup>γ</sup> with *A. eichwaldi* and *Ptychopyge globifrons*.

These investigations were continued by P. Raimond and A.F. Lesnikova. In the Volkhov River section, Raimond established for the first time the following formations: the Volkhov Formation, which corresponds to the B<sub>1</sub> and B<sub>2</sub> zones after Schmidt), Kunda Formation (B<sub>3</sub>), Duboviki and Revel formations (C<sub>1</sub>) (Raymond, 1916; Balashova and Balashov, 1959, 1961). In the same



region Lesnikova recognized the following formations, trilobite zones, and beds with brachiopods: the Volkhovstroi Formation, which is close to the Duboviki Formation in volume, including  $C_1^I$  with *A. eichwaldi*,  $C_1^{II}$  with *A. cornutus*,  $C_1^{III}$  with *A. kowalewskii*; Porogi Formation ( $C_1^{IV-V}$  with the *A. ornatus* Zone); Valim Formation ( $C_1^{VI}$  with the *A. devexus* var. *applanata* Zone); and Vel'sy Formation ( $C_1^{VII}$  with the beds containing *Porambonites janischevskii* and *Christiania oblonga*) (Yanishevskii, 1931; Balashova and Balashov, 1961).

Within the deposits of the Volkhovstroi and Vel'sy formations, Hecker recognized 25 beds on the basis of their lithological characteristics (they are designated by Roman letters from a to z); later, Yanishevskii added one more bed, a<sub>1</sub>. At the beginning of the 1920s when the Volkhov hydroelectric power station was under construction, these beds yielded an immense collection of trilobites, which were studied by Lesnikova and, subsequently, by Balashova. In the lower part of the carbonate section of the Volkhov River, Balashova and Balashov (1959) recognized the following horizons: the Volkhov Horizon with the zones  $B_{II}^{\alpha}$  with *Asaphus priscus*, *Megalaspis planilimbata*, and *M. limbata*;  $B_{II}^{\beta}$  with *A. broeggeri* and *M. hyorhina*;  $B_{II}^{\gamma}$  with *A. lepidurus* and *M. gibba*; and the Obukhovo Horizon with the zones  $B_{III}^{\alpha}$  with *A. expansus* and *A. lamanskii*;  $B_{III}^{\beta}$  with *A. raniceps*;  $B_{III}^{\gamma}$  with *A. major* and *Cyclendoceras cancellatum*; and, in the upper part, the Duboviki Horizon with the following subhorizons and zones: the Volkhovstroi Subhorizon ( $C_1^{\alpha}$  with *A. eichwaldi*, *A. cornutus*, and *A. kowalewskii* zones); Porogi Subhorizon ( $C_1^{\beta}$  with the *A. ornatus* Zone); and Valim Subhorizon ( $C_1^{\gamma}$  with *A. devexus*, *Caryocystites*, and *Ancistroceras*). Following Hecker, Balashova and Balashov (1961) referred the Vel'sy Formation to the Kukery Horizon ( $C_2$ ).

The revision of the 80-year-long stratigraphical research of the carbonate Ordovician deposits of the Ladoga Glint was done by Popov and Männil when preparing the Resolutions of the Interdepartmental Commission on the Stratigraphy of the Ordovician and Silurian in 1984 (*Resheniya...*, 1987). As a result, the stratigraphical scheme has been enriched with the Kunda, Aseri, Lasnamägi, and Uhaku horizons, which were established in Estonia, and the Obukhovo Formation, which consists of the Obukhovo Horizon and the lower half of the Duboviki Horizon as established by Balashova and Balashov, and the zonation, mainly of

the upper Kunda and Aseri parts, has been modified (Table 1). In the same year, the Lynna Formation was established by Mägi (1984a, 1984b).

Presently, the sequence-stratigraphical study aimed at developing a very detailed correlation scheme of the Ordovician sediments of various facial zones of Baltoscandia is under way on the territory of the Ladoga Glint. This study is as yet mainly restricted to the Volkhov Horizon of the Glint (Dronov *et al.*, 1993, 1996, 1998).

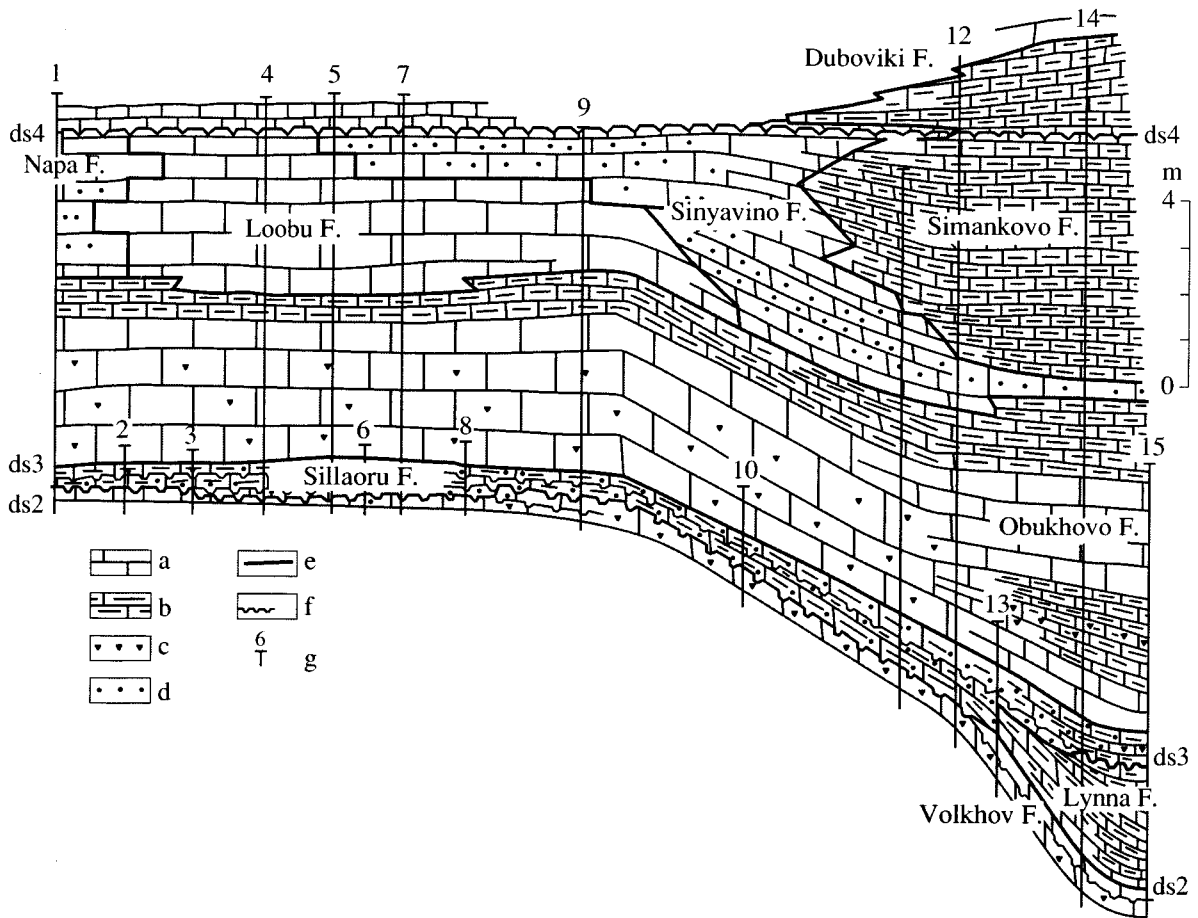
In the 1990s, the stratigraphy of the Ordovician carbonate deposits of this region and the distribution of asaphine trilobites in these deposits were studied by the author (Ivantsov, 1990a, 1993a, 1993b, 1996, 1997a, 1997b; Ivantsov and Mel'nikov, 1993; Ivantsov and Mel'nikova, 1998). The zonal sequence of the upper Volkhovian–Aserian part of the section that is based on the distribution of trilobites of three phylogenetic lines of one genus *Asaphus* represents the main result of this study. The proposed scheme will be discussed below in detail.

### 1.1. Stratigraphic Units of the Carbonate Part of the Ladoga Glint Ordovician

The Early and Middle Ordovician carbonate deposits of the Ladoga Glint fairly considerably differ from the coeval deposits of the Baltic Glint. Their thickness is greater, they are more clayey and less dolomitized and contain fewer beds with glauconite and oolites of brown iron compounds, and these beds thin out eastward (Fig. 2). The Ladoga Glint sections are stratotypic for a number of formations. The stratigraphic sequence of the Glint carbonate deposits assumed in the present paper is slightly different from the widely accepted sequence; below a generalized description of its main units is given.

I define the boundaries of formations and members on the basis of those changes in the material composition of rocks that are macroscopically visible under field conditions. They usually coincide with generally accepted boundaries, although they are rough and approximate in many cases. Some boundaries of horizons and zones are drawn through the regional discontinuity surfaces for which the change in faunistic assemblages has been proved. The development of these surfaces over the entire, sometimes huge, area of their distribution was synchronous in the geological sense; therefore, they allow the most precise correlation of the sections. Since these surfaces are frequently cited in this work, they will be abbreviated as (ds1–ds4).

No individual sections are described here because it is beyond the scope of the present paper. The stratigraphic columns of the main outcrops—Putilovo (Fig. 3), Lava (Figs. 4–9), Voibokalo (Fig. 10), Volkhov (Figs. 11–17), and Lynna (Figs. 18, 19)—are included to demonstrate the distribution of asaphines.

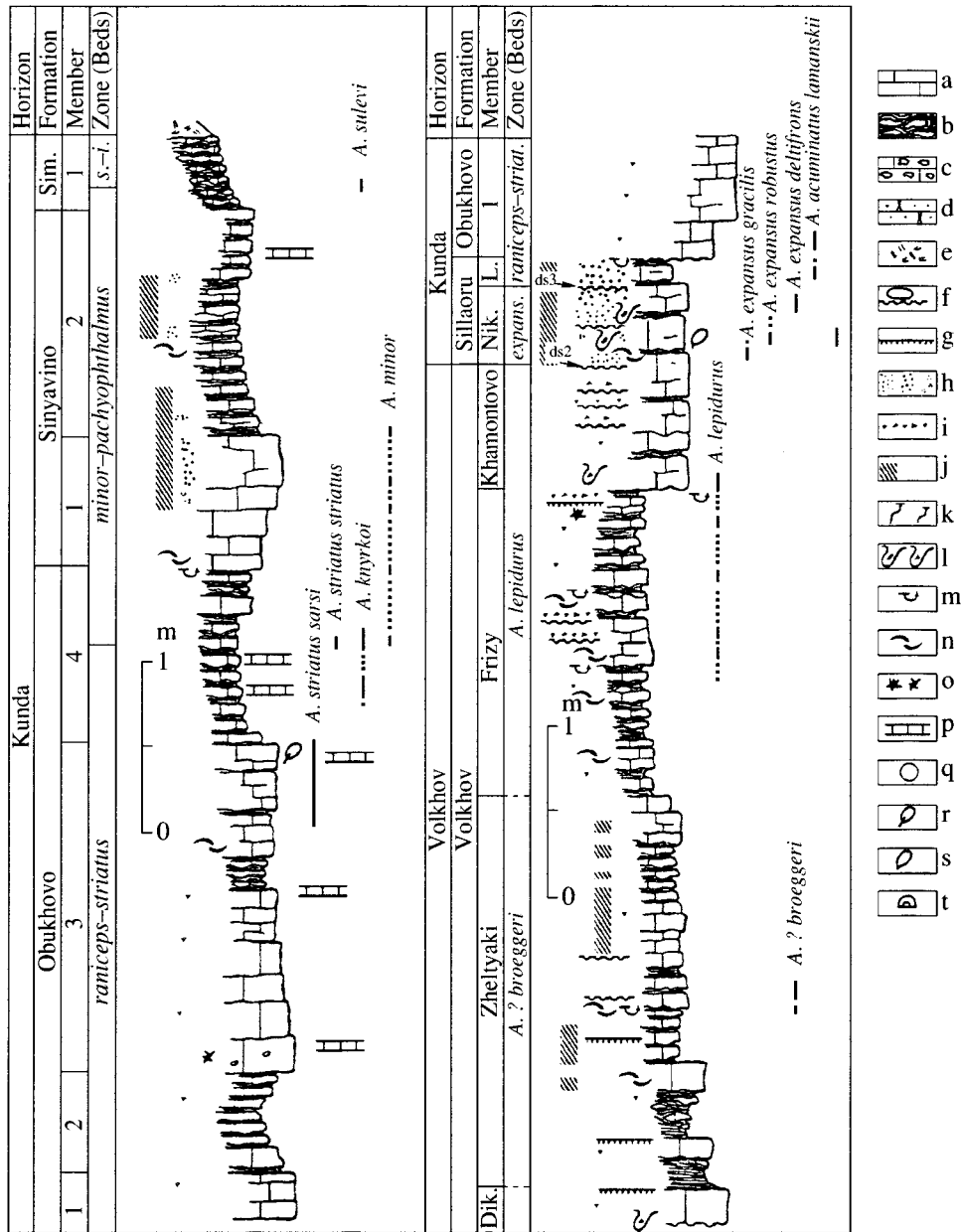


**Fig. 2.** Schematic profile of the Kunda deposits along the Russian part of the Baltic-Ladoga Glint: (a) limestone, (b) clayey limestone and marls with clay interbeds, (c) glauconite, (d) oolites of iron brown compounds, (e) formation boundaries, (f) regional discontinuity surfaces, (g) sections within the Baltic Glint [(1) Narva R., (2) Luga R., (3) village of Kotly, (4) Lomashka R., (5) Koporka R., (6) Voronka R., (7) Ruditsa R., (8) village of Vil'povitsy, (9) Popovka R., (10) Tosna R.] and the Ladoga Glint [(11) Putilovo, (12) Lava, (13) Voibokalo, (14) Volkhov, (15) Lynna]. Abbreviations: (F.) Formation.

**Upper Part of the Latorp Horizon, Volkhov Horizon, and the Lower Part of the Kunda Horizon. The Volkhov Formation.** The holostratotype of this formation was not located, the lectostratotype has been designated in the section of the working quarry near the village of Babino by Dmitrovskaya (1989, 1991) (Babino outcrop, Fig. 11).

The formation is composed of clayey limestone, which is predominantly variegated, thick-bedded to lenslike, organogenous detritic, and contains frequent interbeds of clay and, usually, a large quantity of macroscopic glauconite grains. Different researchers draw the lower boundary of this formation differently: either through the regional ds1 inside thick-bedded limestones (Dikari) (*Resheniya...*, 1987; Popov *et al.*, 1997) or through the floor of these limestones (Dmitrovskaya, 1989, 1991; Dronov, 1998; Dronov *et al.*, 1993, 1996, 1998; Ivantsov, 1997a; Ivantsov and Mel'nikova, 1998; Zaitsev and Baraboshkin, 2000), much as the lower boundary of the coeval Toila Formation has been drawn in Estonia (Mägi, 1984a, 1984b; *Resheniya...*, 1987;

Männil, 1990). The second variant is accepted in this paper. The position of the upper boundary of this formation in the sections along the Volkhov and Syas' rivers has not been identified precisely. It was supposed that it coincides with the floor of the beds with *A. expansus*. When describing the *A. expansus* and *A. lamanskii* Zone, Lamanskii (1905) noted that the lower boundary of this zone coincides with the lilac stripe (ds2 in the present work) inside the lower "white bed," above which an aggregation of small grains of glauconite is observed. Since there are several such stripes inside the lower "white bed," Balashova and Balashov (1959) identified the upper boundary of the Volkhov Horizon regardless of the lithology but based on the first occurrence of *A. expansus*. The opinion of Balashova and Balashov that this species appears on the Volkhov River 3 m above the floor of the lower "lenticular bed" (i.e., the Sillaoru Formation) is not quite correct. The thickness of rocks located between the "white" and "lenticular" beds is greatly variable in the Volkhov section and reduces upstream by 0.5 m; there-



**Fig. 3.** Distribution of trilobites of the subfamily Asaphinae in the Putilovskii Kar'er section (acting quarry 1–2 km west of the Putilovo village, the stratotype of the Sinyavino Formation). Designations: (a) limestone, (b) lenslike laminated limestone with clay interbeds, (c) limestone with cavities of leaching, (d) sandstone, (e) soil, (f) discontinuity surface with pebbles, (g) discontinuity surface represented by hardground with *Trypanites* borings, (h) oolites of iron brown combinations, (i) visible grains of glauconite, (j) red coloration, (k, l) vertical digging holes; (k) thin and long holes, (l) short and wide *Bergaueria*-type holes filled with oolites or glauconite grains, (m) ichnofossils on a unit floor, (n) aggregation of large fragments of trilobite carapaces, (o) iron pyritis concretions, (p) nautilid shell fragments, (q) echinospherite skeletons. (r–t) finds of fauna in living positions: (r) lingulids, (s) articulate brachiopods, (t) bun-shaped bryozoan colonies. Abbreviations: (Sim.) Simankovo Formation, (Dik.) Dikari, (Nik.) Nikol'skoe Member, (L.) Lopukhinka Member, (s.-i.) *sulevi-ingrianus* Zone.

fore, the level of the mark “3 m below the lower lenticular bed” can vary within the Volkhov Formation depending on the outcrop (Ivantsov, 1993b). In the present paper, the upper boundary of the Volkhov Formation in the sections along the Volkhov and Syas' rivers is drawn through the roof of the thick-bedded limestone member, which is approximately 15–20 cm above

ds2 (Figs. 11, 12, 18). This member (Lamanskii's lower “white bed”) is exposed as a scarp in all outcrops of the Volkhovian–Kundian deposits along the Volkhov, Syas', and Lynna rivers, and is a good marker. Its thickness is about 0.5–0.6 m. Taking into account the special significance of this member and the usual practice of the literature on the Baltic Ordovician, this member has

been given a proper geographical name, Khamontovo, after the village of Khamontovo on the Syas' River, because in outcrops around this village this member is most obviously exposed (Ivantsov, 1993b, 1997; Ivantsov and Mel'nikova, 1998). Thus, the upper boundary of the Volkhov Formation is somewhat higher than the upper boundary of the Volkhov Horizon in the sections along the Volkhov and Syas' rivers. The boundary of the formation coincides with that of the horizon in the sections situated west of the Volkhov River (Figs. 3–5, 10). The boundary of the horizon is drawn through the floor of the "lower lenticular bed" by all authors.

The Volkhov Formation (delineated in accordance with our understanding of its boundaries) includes the members of Dikari (with Päite and Saka submembers), Zheltyaki, Frizy, and Khamontovo. The names of Dikari, Zheltyaki, and Frizy were given by workers of the Putilovo and Volkhov quarries for units of the glauconite limestone; they were introduced into the literature by Lamanskii and became generally accepted informal names of subhorizons (Balashova and Balashov, 1959), subformations (Zaitsev and Baraboshkin, 2000), beds (Popov *et al.*, 1997), or members of the Volkhov Horizon (Dronov *et al.*, 1996; Ivantsov and Mel'nikova, 1998). Since their lithological volumes have not changed since Lamanskii's time, these original names may be kept and used for the designation of members.

The lower half of the formation is abundant in various discontinuity surfaces, which usually change their appearance within a short distance. Thus, their identification and tracing are obstructed. Currently, only one surface (ds1) representing the lower boundary of the Volkhov Horizon has practical importance among numerous discontinuity surfaces. This surface is situated inside the series of the thick-bedded limestone at the base of the carbonate section and at the roof of the Päite Submember (Figs. 4, 11) (Orviku, 1960a, 1960b; Mägi, 1984a, 1984b; Dronov *et al.*, 1993, 1996; Ivantsov, 1997; Ivantsov and Mel'nikova, 1998). It may be either irregular, corroded, with amplitude of irregularities reaching 3–4 cm and with large detached masses or ideally smooth with small discs of echinoderm cirri and widely scattered large burrows (or borings?) of irregular shape. In Lamanskii's time (Lamanskii, 1901, 1905), workers called it "glass." The roof of underlying rocks is rusty yellow for several centimeters, and the surface, which can usually be easily prepared, itself looks velvety green owing to a dense admixture of fine glauconite grains. In addition to detached masses, small pebbles are occasionally observable immediately above this surface (for example, in the Gorodishche outcrop, Fig. 4). It passes into a smooth surface with amphora-shaped boring holes (Orviku, 1960a, 1960b) in the Baltic Glint, where it coincides with the lower boundary of *Megistaspis polyphemus*.

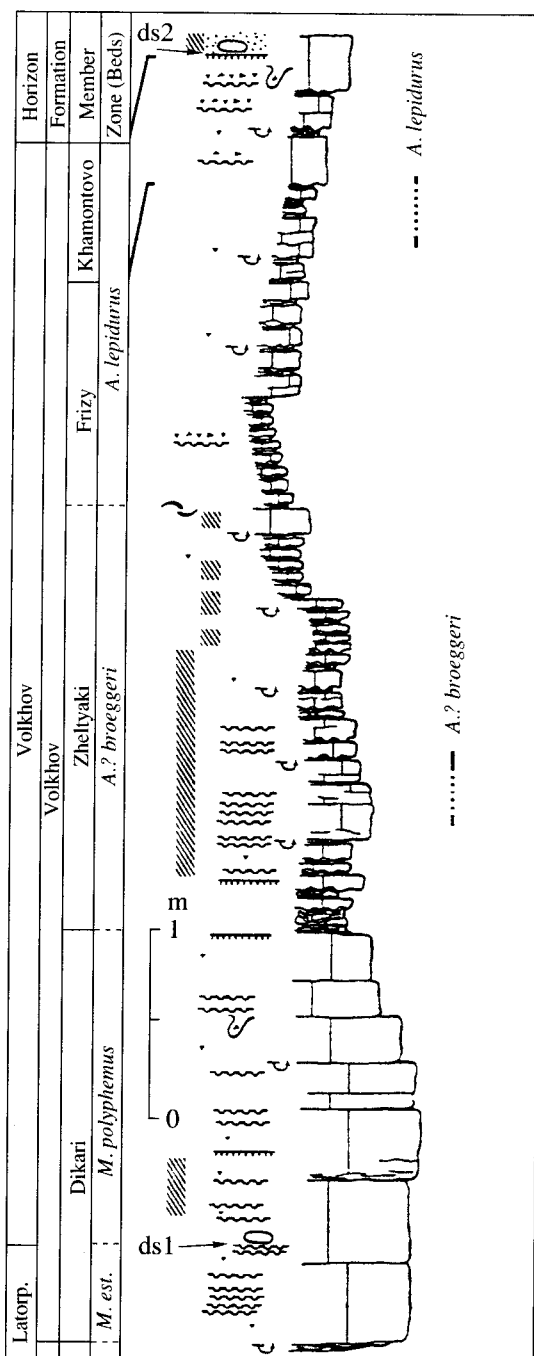


Fig. 4. Distribution of trilobites of the subfamily Asaphinae in the Gorodishche outcrop (right bank of the Lava River below the village of Gorodishche). Designations as in Fig. 3. Abbreviations: (*M. est.*) beds with *Megistaspis estonica*.

The next chain of discontinuity surfaces is situated in the roof of the Volkhov Formation. These are surfaces with a small amplitude of irregularities and aggregations of glauconite grains and organic detritus above them; the roof of the underlying beds is lilac gray. The uppermost surface of this series (ds2) is most important. Within the Ladoga Glint, it is characterized by the

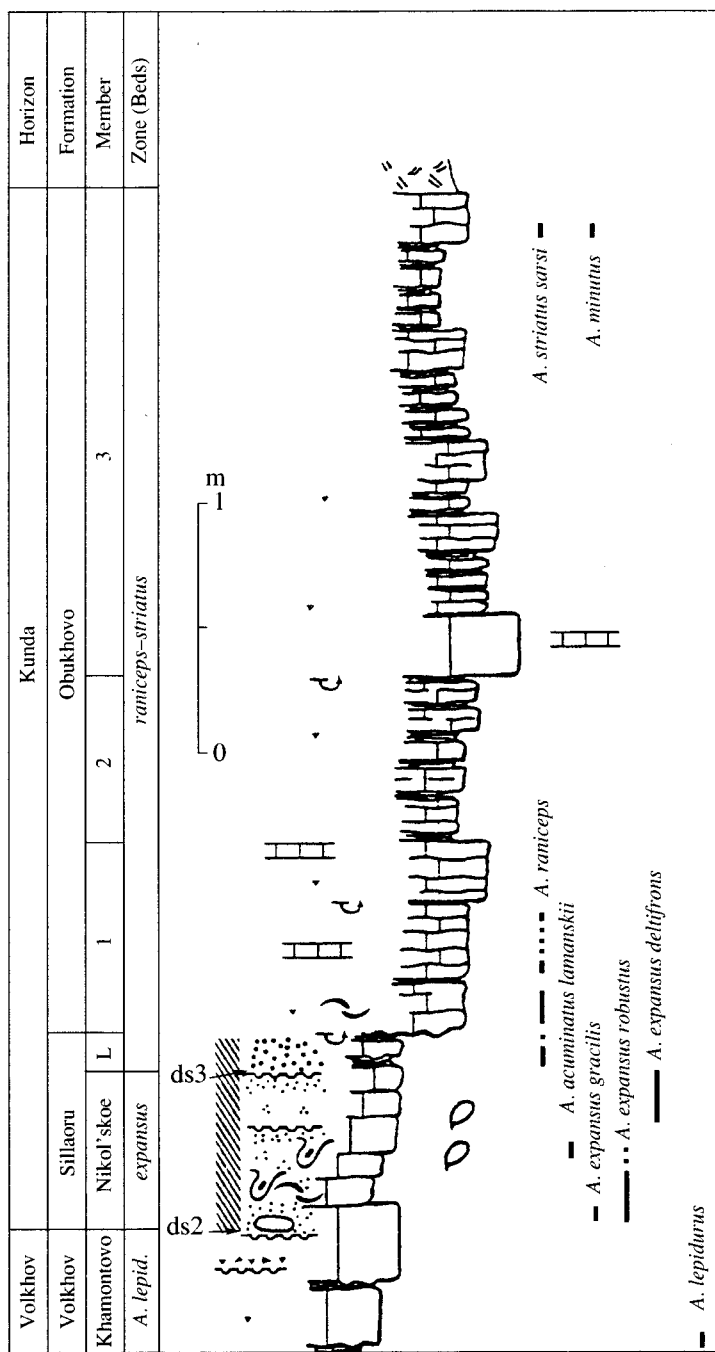


Fig. 5. Distribution of trilobites of the subfamily Asaphinae in the Gorodishchenskii Kar'er outcrop (abandoned quarry on the left bank of the Lava River opposite to the village of Gorodishche, stratotype of the Nikol'skoe Member of the Sillaoru Formation). Designations as in Fig. 3. Abbreviations: (L.) Lopukhinka Member, (A. lepid.) beds with *Asaphus lepidurus*.

lilac gray color of the underlying rocks and rare borings of *Trypanites*. In the sections along the Volkhov and Syas' rivers, the floor of the overlying rocks is abundant in small glauconite grains and fragmentary organic remains (Figs. 11, 18), and on the territory between the station of Voibokalo and the village of Putilovo, it is abundant in small oolites of brown compounds of iron and rare pebbles of glauconite limestone with a rusty

yellow bordering (Figs. 3, 5, 10). Farther to the west, the coloration of the roof of the underlying rocks transforms into red (Tosna River) and then into rusty yellow (Popovka River and area to the west of it), *Trypanites* borings become more frequent, and the abundance of glauconite limestone pebbles increases. This boundary retains its appearance up to the village of Iru in Estonia (Orviku, 1960a, 1960b). The lower boundary of

*A. expansus* coincides with ds2 (Lamanskii, 1901, 1905; Ivantsov, 1990a, 1993b) and delineates the lower boundary of the Kunda Horizon (Orviku, 1960a, 1960b; Mägi, 1984a, 1984b; Ivantsov, 1993b; Männil, 1990).

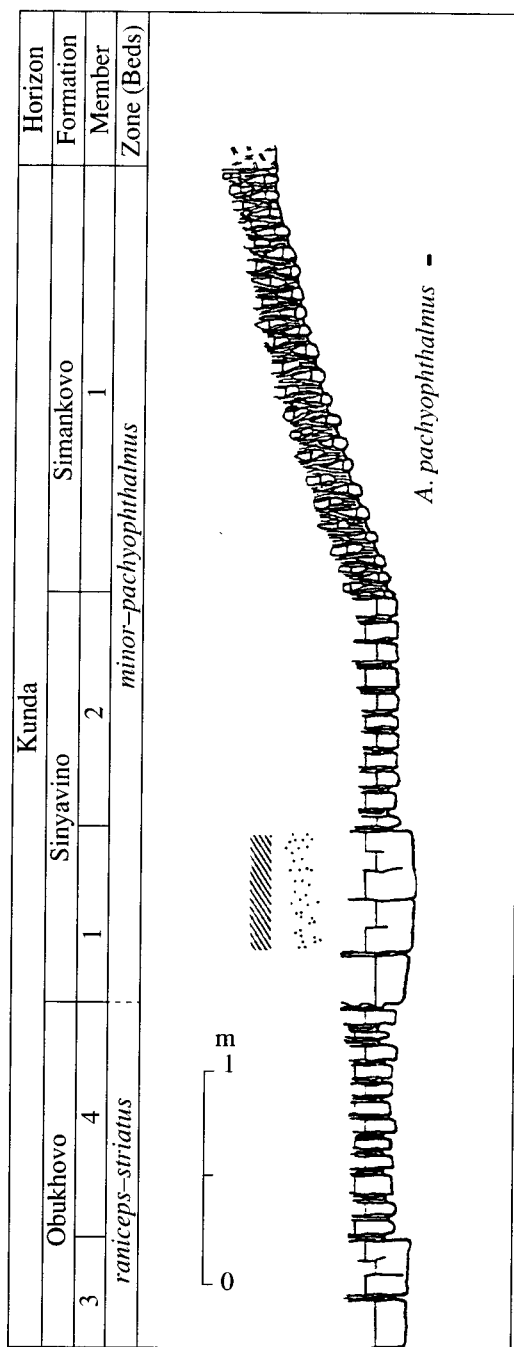
The thickness of this formation on the Syas' River (right bank near the railroad bridge in the village of Chernetskoe) is 6.8 m, that on the Volkhov River (lectostratotype) is about 6.5 m, that on the Lava River (right bank below the village of Gorodishche) is 6.8 m, that in the Putilovo Quarry is 6.9 m. The latter figure has been obtained by combining our data on the thickness of the unit between the floor of the Sillaoru Formation and the roof of the Dikari Member and data provided by the Putilovo Quarry administration on the thickness of the commercial unit ("Dikari"). This formation covers the entire Ladoga Glint. The Toila Formation is a time analogue of the Volkhov Formation on the Baltic Glint.

**Kunda Horizon. Lynna Formation.** The stratotype of this formation is situated on the left bank of the Lynna River several tens of meters upstream of its mouth (Lynna Mouth outcrop, Fig. 18).

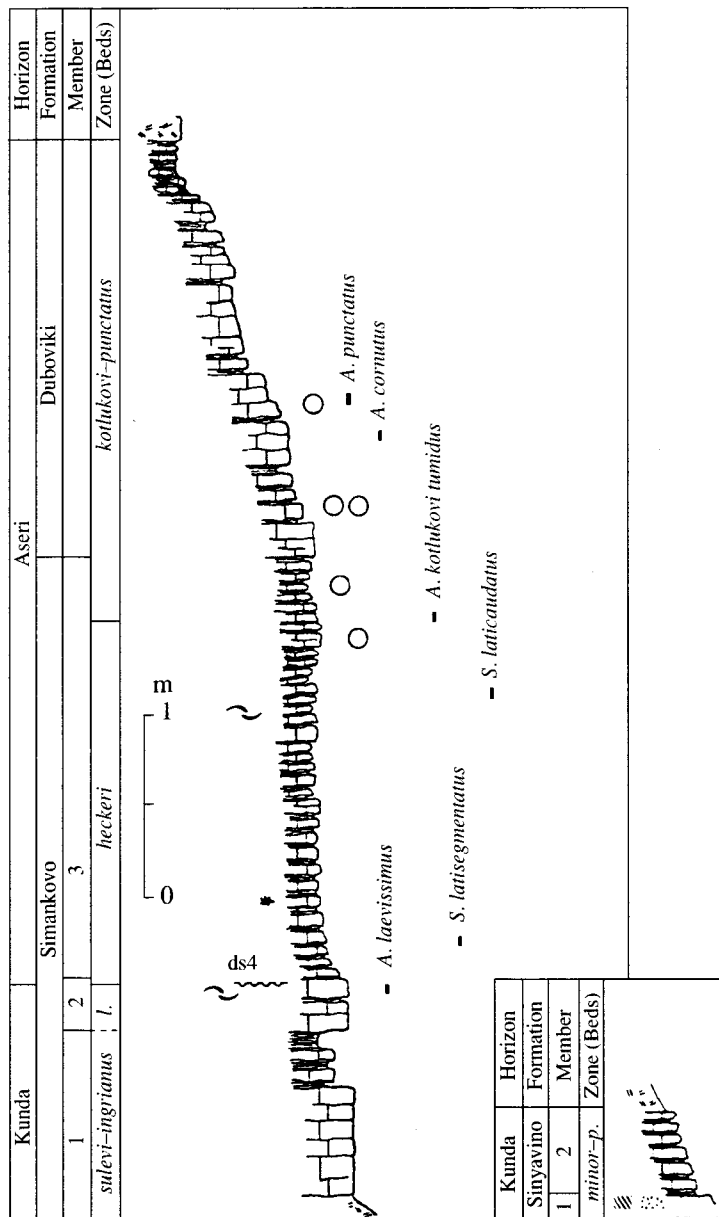
This formation is represented by clayey limestone and marls with frequent clay interbeds. Rare macroscopic glauconite grains occur at the base of the formation only. Under the name of the Lynna Formation, Mägi (1984a) combined gray clayey limestone of the upper part of the Volkhov Horizon (Syas' Member) and the lower part of the Kunda Horizon (Lava Member), which is bordered below by variegated Zheltyaki Limestone and above by oolitic limestone of the Sillaoru Formation. However, the limestone of the Syas' Member, i.e., the Frizy and Khamontovo members, is less clayey in comparison with the overlying rocks and contains glauconite grains, which are especially abundant above the discontinuity surfaces. On the basis of these characters, they resemble the Volkhov Formation whereas the Lava Member sediments (absent from the Lava River?) are clayey to marls, with red surfaces of discontinuity, and are closer to the Sillaoru Formation, but are barren of oolites. Therefore, the traditional association of Dikari, Zheltyaki, and Frizy is restored; the Lynna Formation is kept, but its lower boundary is drawn through the roof of the Khamontovo Member.

This formation includes two members. The lower member is composed of greenish gray, lenslike laminated marl with frequent clay interbeds. Small glauconite grains are common at the base of the member. The thickness of the member in the stratotype is 2.2 m, that on the Volkhov River is 2.3 m (right bank, southern outskirts of the village of Obukhovo) or 1.7 m (left bank near the northern outskirts of the village of Zvanka). The upper member is composed of clayey, medium-laminated, greenish gray or lilac gray limestone, which rarely contains crimson and brick-red stains with thin interbeds of clay. Small aggregations of fine oolites occasionally occur in the roof of the member. The

member contains discontinuity surfaces of predominantly lilac gray color, with aggregations of dispersed trilobite remains above them. The upper surface of this series (ds3) on the Volkhov and Syas' rivers has a brick-red roof of underlying rocks with rare *Trypanites* borings and a small amplitude (a few millimeters) of irregularities. Above are aggregations of fine (up to 1 mm



**Fig. 6.** Distribution of trilobites of the subfamily Asaphinae in the Vasil'kovo outcrop (left bank of the Lava River near the northern outskirts of the Vasil'kovo (Troitskoe) village). Designations as in Fig. 3.

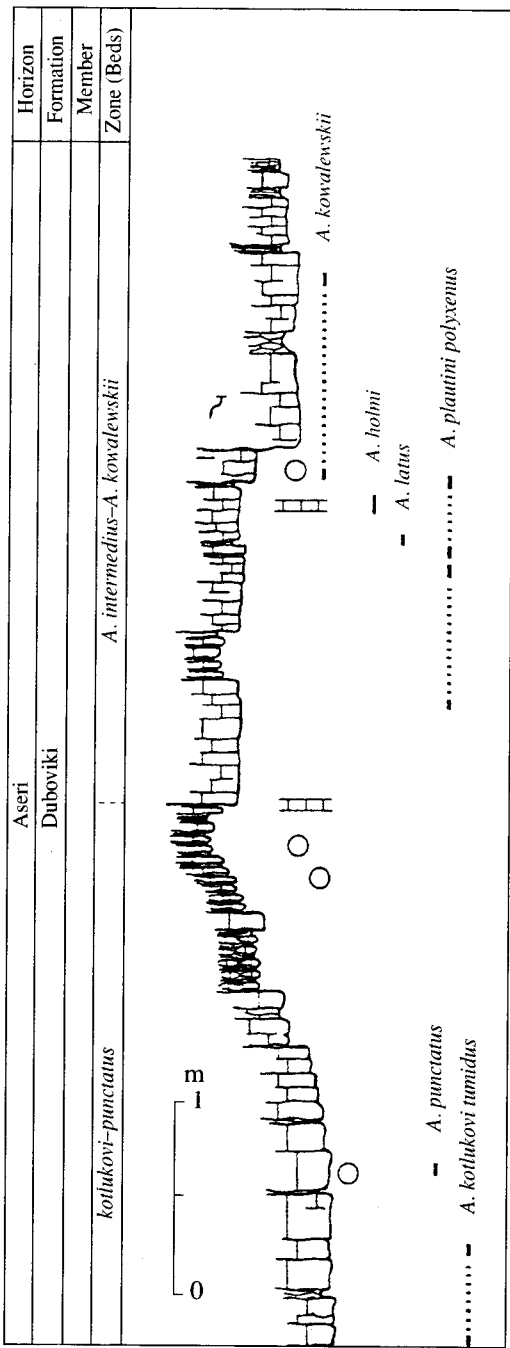


**Fig. 7.** Distribution of trilobites of the subfamily Asaphinae in the Kavra outcrop (right bank of the Lava River, about 200 m downstream of the Kavra River mouth). Designations as in Fig. 3. Abbreviations: (*l.*) *laevisissimus* Zone, (*minor-p.*) *minor-pachyophthalmus* Zone.

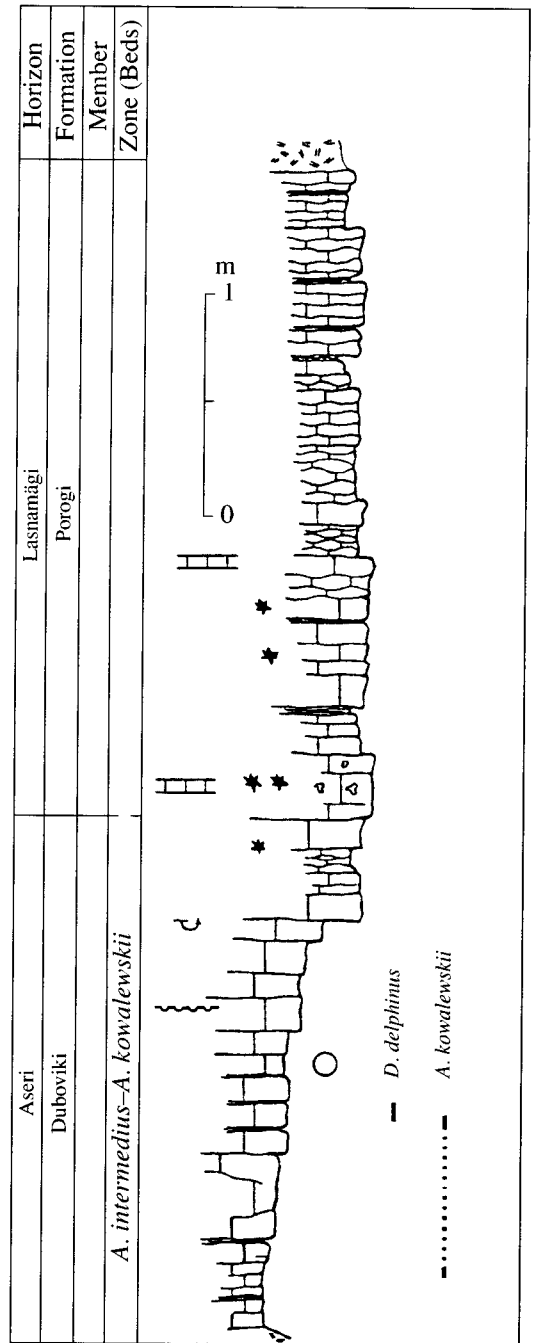
diameter) oolites of brown compounds of iron belonging to the Sillaoru Formation (Figs. 12, 18, 19). This surface migrates to the middle part of the Sillaoru Formation near the station of Voibokalo and westward and is represented by a chain of low outliers with a light gray color from the constituting rocks. The overlying rocks are abundant in large (up to 2.5 diameter) well-developed oolites (Figs. 3, 5, 10). This surface retains its appearance along the Baltic Gint at least as far as the village of Toila in Estonia. The lower margin of the *A. raniceps* range and the upper margin of the *A. expansus* range coincide with ds3 (Ivantsov, 1990a). The

thickness of this member is 0.5 m in the stratotype, 0.2 m near the southern border of the village of Obukhovo on the Volkhov River, and 0.35 m near the northern outskirts of the village of Zvanka.

The total thickness of the Lynna Formation in the Syas' River basin is 2.7 m, that on the Volkhov River is from 2.5 m in the northern part to 2.05 m in the southern part of the outcrops. This formation occurs in the basins of the Syas' and Volkhov rivers and gives way to the Nikol'skoe Member of the Sillaoru Formation on the west.



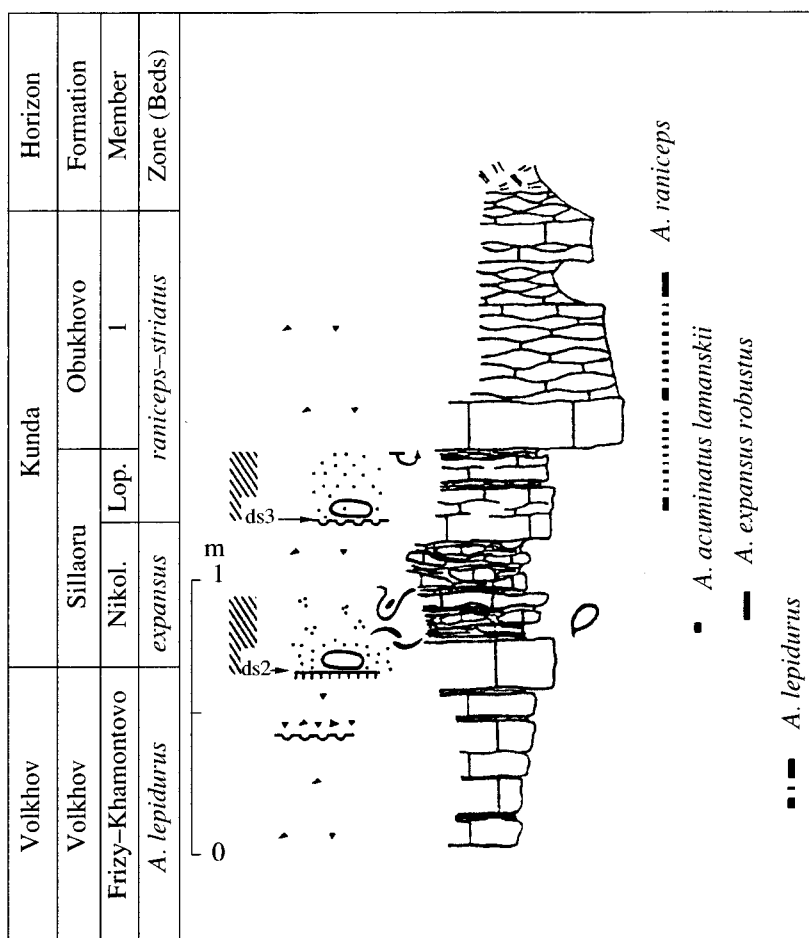
**Fig. 8.** Distribution of trilobites of the subfamily Asaphinae in the North Naziya outcrop (left bank of the Lava River near the northern outskirts of the Naziya village). Designations as in Fig. 3.



**Fig. 9.** Distribution of trilobites of the subfamily Asaphinae in the South Naziya outcrop (left bank of the Lava River, 50–100 m upstream of the auto-bridge in the Naziya village). Designations as in Fig. 3.

**Sillaoru Formation.** The name was proposed by Männil and Rõõmusoks to designate the lower series of rocks with oolites of brown compounds of iron (so called lower “lenticular bed”). The stratotype of this formation is situated in Estonia on the left bank of the Purtse River near the village of Sillaoru (Männil and Rõõmusoks, 1984).

The formation is represented by clayey limestone, marl, and clay, which usually abound in oolites of various sizes and stages of development. However, individual beds may be barren of oolites but contain glauconite; in some parts of the Pada Limestone in Estonia (Orviku, 1960a, 1960b) and in Member 2 on the Lynna River (see below). The first occurrence of oolites of the



**Fig. 10.** Distribution of trilobites of the subfamily Asaphinae in the Voibokalo outcrop (abandoned quarry at the railway station of Voibokalo, at the intersection near the village of Sibola). Designations as in Fig. 3. Abbreviations: (Nikol.) Nikol'skoe Member, (Lop.) Lopukhinka Member.

Sillaoru Formation coincides with discontinuity surfaces, therefore the lower boundary of the formation is everywhere drawn through these surfaces, ds3 in the eastern part of the Ladoga Glint (by the station of Voibokalo) (Figs. 12, 18, 19) and ds2 in the western part (Figs. 3–5, 10). To the west, the Sillaoru Formation is traced up to the village of Iru in Estonia (Orviku, 1960b) to gradually give way to the Lynna Formation east of the Voibokalo station (Fig. 2). This formation includes the Nikol'skoe and Lopukhinka members in the western part of its area (up to the station of Voibokalo) (Ivantsov, 1990a) and unnamed Members 1 and 2 east of the Voibokalo station. The Nikol'skoe Member is composed of greenish or rosy gray clayey limestone and marl, occasionally with brick-red stains. Its stratotype is situated in the quarry on the left bank of the Lava River opposite the village of Gorodishche (Gorodishchenskii Kar'er outcrop, Fig. 5). Small, less than 5 cm in diameter, glauconite limestone pebbles with an ochreous rusty yellow surface and *Trypanites* borings rarely occur in the floor of the member (much less than

1 mm) gradually increase upsection, reaching up to 1–1.5 mm in diameter near the roof. The thickness of the member varies from 0.45 m at some places near the village of Putilovo to 0.6 m at the Lava River and 0.5 m in the quarry by the station of Voibokalo. The Lopukhinka Member is usually composed of a rather thick bed of gray clay (up to 10 cm) overlain by gray clayey limestone. Both of the beds are filled with large (up to 2.5 mm in diameter) well-formed oolites resembling lentils in their shape, coloration, and size; owing to the latter, this and all other beds with oolites in the Leningrad Region have been named "lenticular beds." Small pebbles of the limestone with large oolites are present in the lower part of the member in the quarry near the station of Voibokalo (Fig. 11). The thickness of the member varies from 0.14 to 0.18 m around the village of Putilovo and the Lava River to 0.3 m in the quarry near the station of Voibokalo. This section of the formation is somewhat different in the basins of the Volkhov and Syas' rivers. Unnamed Member 1 is composed of gray, rosy gray, medium-laminated clayey limestone with clay interbeds. Oolites are abundant,

although very small (Figs. 12, 19). The thickness of this member varies from 0.25 m to 0.35 m, decreasing to 0.05–0.03 m on the Syas' River at the Lynna River mouth and downstream of it. In the latter case, the member is represented by brick-red clay, with oolites that can only be revealed after elution (Fig. 18). Unnamed Member 2 is composed of gray, greenish gray, medium-laminated limestone with clay interbeds. This member is crowned with a gray, patchy cherry-red clay bed of up to 0.1 m, occasionally with a lenslike marl interbed. The red coloration is either associated with the lower half of the bed or surrounds marl lenses. Oolites are usually absent from deposits of this member, but its upper two-thirds are filled with oolites in a number of outcrops along the Lynna River, 1–1.5 km upstream of its mouth (Fig. 19), and the Syas' River, 0.5–1 km upstream of the Lynna River mouth. Small macroscopic glauconite grains have been recorded in the middle part of this member in outcrops along the Syas' River at the Lynna River mouth and downstream of it. The thickness of the member is 0.27 m near the northern outskirts of the village of Zvanka, 0.4 m near the village of Stuglevo (the member is not traced to the north, in the quarries near the village of Obukhovo) on the Volkhov River, and 0.35–0.7 m in the basin of the Syas' River. On the Ladoga Glint, the total thickness of the Sillaoru Formation varies from 0.6 m in some places near the village of Putilovo to 0.8 m at the Lava River and in the quarry near the station of Voibokalo and from 0.35 m near the village of Obukhovo on the Volkhov River to 0.6–0.65 m near the villages of Stuglevo and Zvanka and 0.75 m in the basin of the Syas' River.

**Obukhovo Formation.** The holostratotype of this formation has not been designated. Balashova and Balashov (1959) indicated the right bank of the Volkhov River near the villages of Obukhovo and Simankovo as the type region of the Obukhovo Horizon, where its thickness is maximal according to these authors. In this region, both the lower and upper boundaries of the formation, even assuming our strict understanding of this formation, are only observable below the village of Simankovo in the old quarry walls and clear spaces for boat sheds. The only full section of the Obukhovo Formation is exposed on the left bank of the Volkhov River in a trench of sewage disposal construction near the northern border of the village of Zvanka; this section was proposed by the author as a lectostratotype of this formation (Ivantsov and Mel'nikova, 1998) (Zvanka outcrop, Fig. 12).

This formation is predominantly composed of medium- and thick-bedded clayey limestone, which can be occasionally weakly dolomitized. Small macroscopic glauconite grains occur in the lower part of this formation, their number decreases to the east and, in the same direction, the micaceous component increases in individual beds and members.

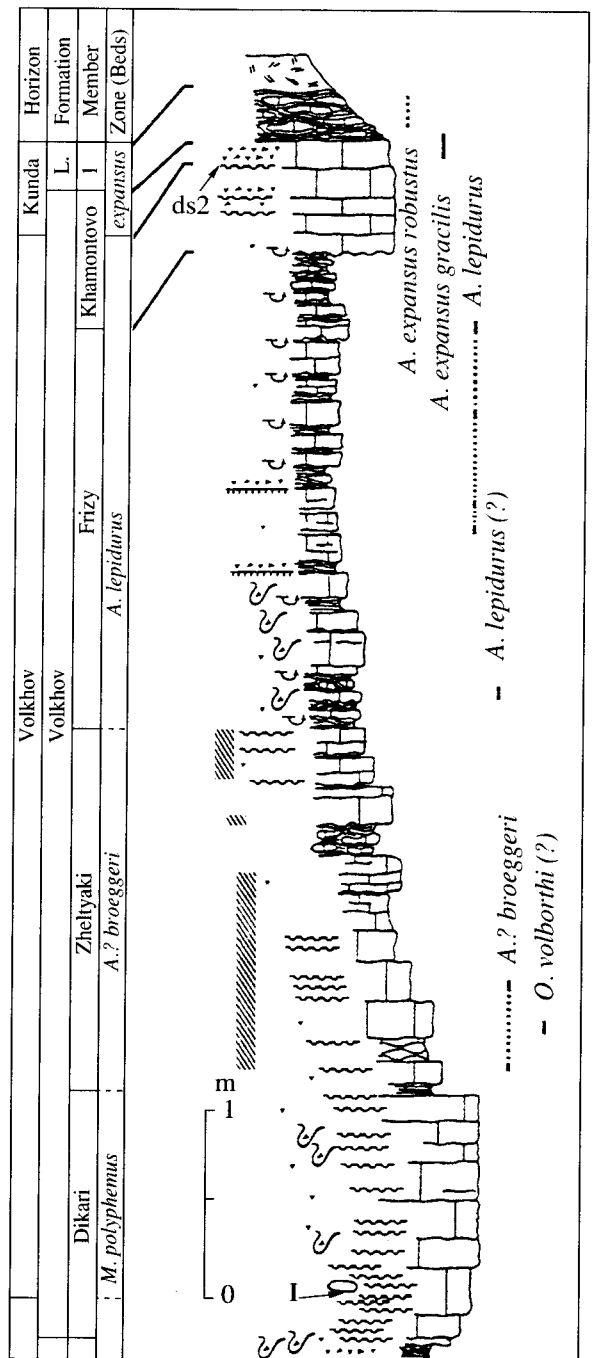
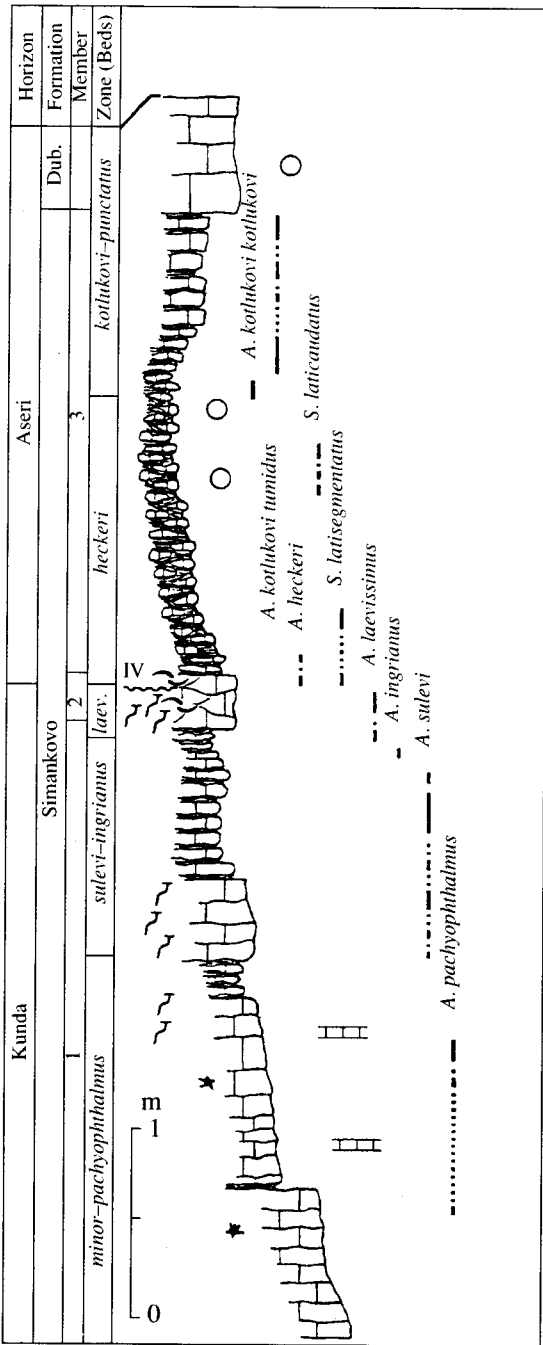


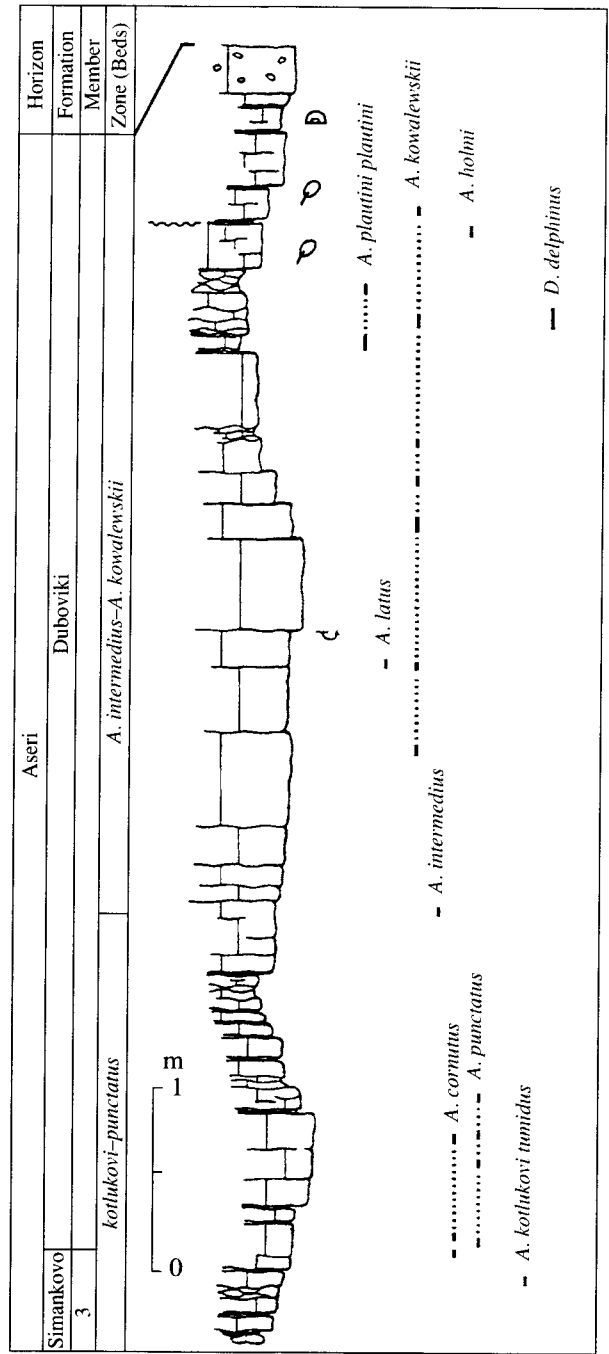
Fig. 11. Distribution of trilobites of the subfamily Asaphinae in the Babino outcrop (right bank of the Volkhov River, quarry near the village of Babino, central part of working area, Volkhov Formation lectostratotype, lectostratotype of the beds with A.? broeggeri). Designations as in Fig. 3. Abbreviations: (L.) Lynna Formation.

In Resheniya... (1987), the lower boundary of the Obukhovo Formation is defined by the first occurrence of *A. expansus*. However, characteristic beds with oolites belonging to the Sillaoru Formation were deposited immediately or at some distance above this event.





**Fig. 13.** Distribution of trilobites of the subfamily Asaphinae in the Volkhov hydroelectric power station dam outcrop (left bank of the Volkhov River, town of Volkhov, 50–200 m downstream of the Volkhov hydroelectric power station dam, stratotype of the *sulevi-ingrianus*, *laevissimus*, *heckeri*, and *kotlukovi-punctatus* zones). Designations as in Fig. 3. Abbreviations: (Dub.) Duboviki Formation, (*laev.*) *laevissimus* Zone.



**Fig. 14.** Distribution of trilobites of the subfamily Asaphinae in the Duboviki Formation (right bank of the Volkhov River, town of Volkhov, 50–150 m downstream of the Volkhov hydroelectric power station dam sluice, lectostratotype of the Duboviki Formation, stratotype of the beds with *A. intermedius*–*A. kowalewskii*). Designations as in Fig. 3.

ovo. In *Resheniya*..., the upper boundary of the Obukhovo Formation is recognized considerably higher, in the roof of the lumpy limestone of the Simankovo Member. This second boundary is recovered on

the Volkhov River several kilometers upstream of the village of Simankovo, downstream of the Volkhov hydroelectric power station dam on the right bank and upstream of a new bridge for car traffic in the town of

Volkhov on the left bank. Taking into account that in the case of the second variant of the boundary the beds with oolites of the upper "lenticular bed" being recognized in other places as an independent unit [Napa Formation (Männil, 1990) or Kandle Formation (Mägi, 1984a, 1984b)] turn out to be included in the Obukhovo Formation, I am turning back to Balashova and Balashov's conclusion and restricting the volume of the Obukhovo Formation.

This formation includes the following four members (upsection):

Member 1, which is represented by dense, thick-bedded limestone that is light gray and pure at the base of the member and lilac gray and clayey in its upper part. Small macroscopic glauconite grains occur throughout the entire member in sections along the Lava River and in the quarry near the village of Putilovo. The average thickness of the member is 0.7–0.75 m.

Member 2, which is represented by greenish, lilac gray, thin-bedded to lens-shaped, clayey limestone with clay interbeds; glauconite grains occur throughout the entire member or in its central part only (eastern margin of the Ladoga Glint). On the Volkhov River, the total thickness of Members 1 and 2 is 2.15 m at the northern border of the village of Zvanka and 3.1 m near the southern border of the Obukhovo village (the thickness increases due to a general trend to the north and at the expense of the upper member of the Sillaoru Formation, which cannot be traced); the thickness is 2.7 m near the bridge across the Lynna River; 1.4 m, near the village of Gorodishche on the Lava River; and 1.3 m, in the abandoned quarry near the village of Putilovo.

Member 3, which is represented by gray, greenish gray, lilac gray, thick-bedded, clayey (occasionally dolomitized) limestone with thin interbeds of clay. A bed of light gray, dense limestone with small holes (leaching cavities) (a so-called "white bed," the floor of  $B_{III}^Y$  after Lamanskii (1901, 1905)) is present at the base of the member. This bed is easily traceable throughout the Ladoga Glint. Macroscopic glauconite grains occur only in the lower quarter of the member and only in the sections along the Lava River and near the village of Putilovo. The thickness of this member is 2.4 m in the stratotype; 2.35 m, on the Lynna River near the bridge; 1.95 m, near the village of Gorodishche on the Lava River and in old quarries near the village of Putilovo.

Member 4, which is represented by limestone, which is usually greenish, lilac gray, thin-bedded to lenslike, clayey, with frequent interbeds of gray clay; this is a characteristic marking member traceable over the major part of the Baltic–Ladoga Glint. The thickness of this member is about 2.35 m in the type section; 0.15 m, near the bridge across the Lynna River (erased by a pre–Upper Devonian washout); 1.1 m, in the northern outskirts of the village of Vasil'kovo on the Lava

River; and 1 m, in the quarry near the village of Putilovo.

The total thickness of the Obukhovo Formation is 5.2 m (4 m excluding the basal part of Member 4) on the Lynna River, from 6.9 m in the southern part of the exposure to 7.85 m in the northern part of the exposure on the Volkhov River; 4.45 m, on the Lava River; and 4.25 m, near the village of Putilovo. This formation is distributed everywhere within the Ladoga Glint.

Partly, the Loobu Formation is a time analogue of the Obukhovo Formation within the Baltic Glint; Members 1–3 of the Obukhovo Formation correspond to the Utria Member and Member 4 corresponds to the lower part of the Valgejõe Member.

**Sinyavino Formation.** This formation was established by the author (Ivantsov and Mel'nikova, 1998). Its stratotype is situated in an abandoned part of the quarry near the village of Putilovo (Putilovo outcrop, Fig. 3).

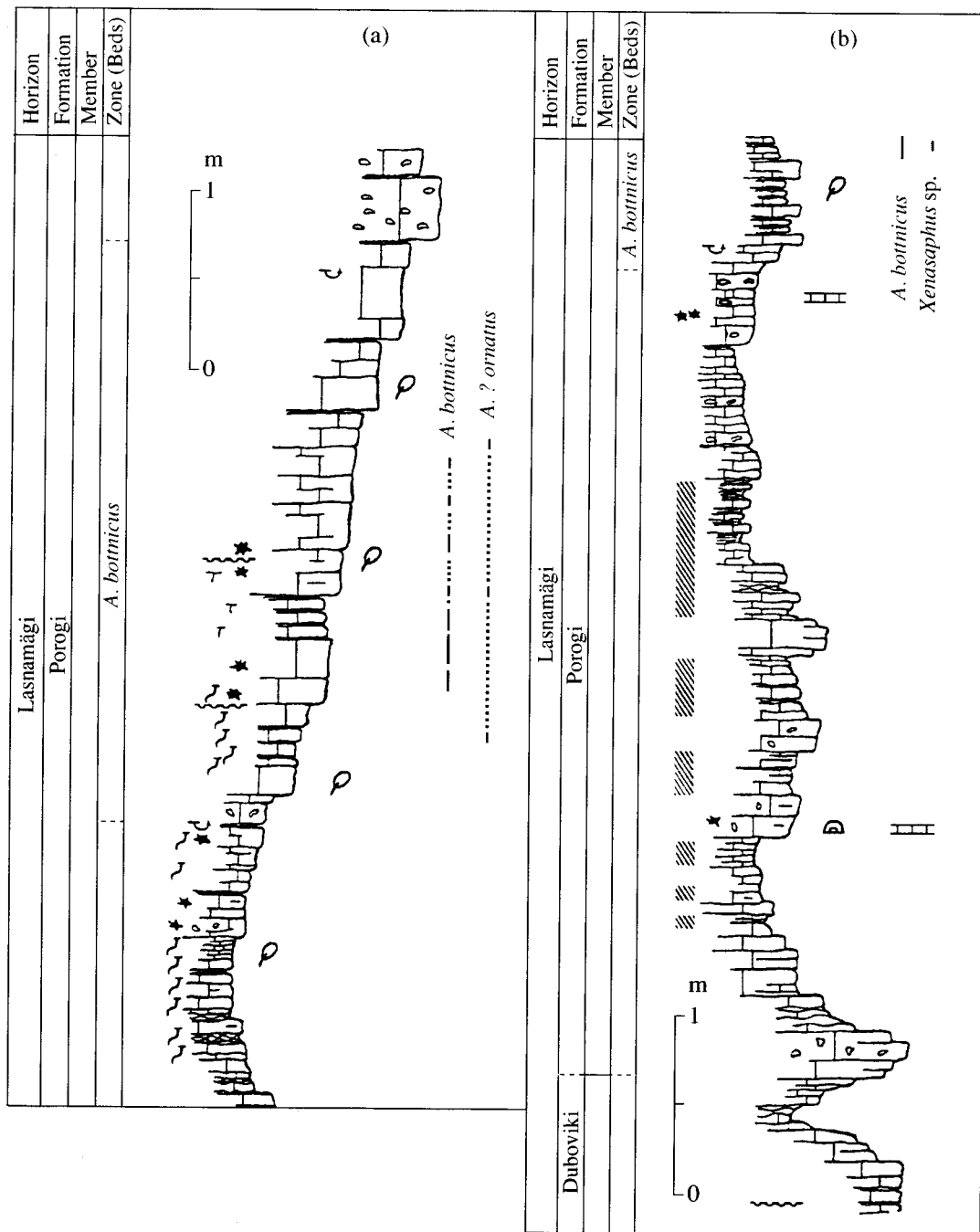
The lower boundary of this formation is recognized in the floor of thick-laminated limestone, the upper part of which usually contains oolites of brown combinations of iron. This formation includes two members (upsection):

Member 1, which is represented by gray thick-laminated limestone, which is tobacco-colored or brick-red with the presence of oolites; in the stratotype section, oolites are large (up to 3 mm diameter) and fully developed; the thickness is 0.8 m in the stratotype; 0.5 m, at the northern border of the village of Vasil'kovo on the Lava River; 0.75 m, within the boundary of the Volkhov town on the Volkhov River (the thickness of the bed with oolite is 0.13 m); and 0.25 m, near the village of Plekhanovo.

Member 2, which is represented by gray or rosy gray (brick-red at the presence of oolites), medium-laminated, clayey limestone with bands of clay; oolites are small, occur at individual levels; the thickness is 1.4 m in the stratotype (oolite levels are 0.75 and 1.1 m above the floor of the member) and 1.1 m near the northern border of the village of Vasil'kovo on the Lava River.

The thickness of the Sinyavino Formation varies from 0.25 m in the northern part of the exposure to 0.75 m in the southern part on the Volkhov River; 1.6 m, on the Lava River; and 2.2 m, near the village of Putilovo. Along the Glint, this formation is traceable to the Volkhov River in the East, where the last oolites are recorded in a single place, 100–150 m upstream of an old auto-bridge on the left bank, inside the boundary of the Volkhov town; this place was discovered by Yanishevskii and Lesnikova (Yanishevskii, 1931). The lower part of the Napa Member (Mägi, 1984a) or Napa Formation (Männil and Rõõmusoks, 1984; Männil, 1990) is a time analogue of this formation in Estonia.

**Upper part of Kunda–lower part of Aseri horizons. Simankovo Formation.** This formation was established by the author (Ivantsov and Mel'nikova,



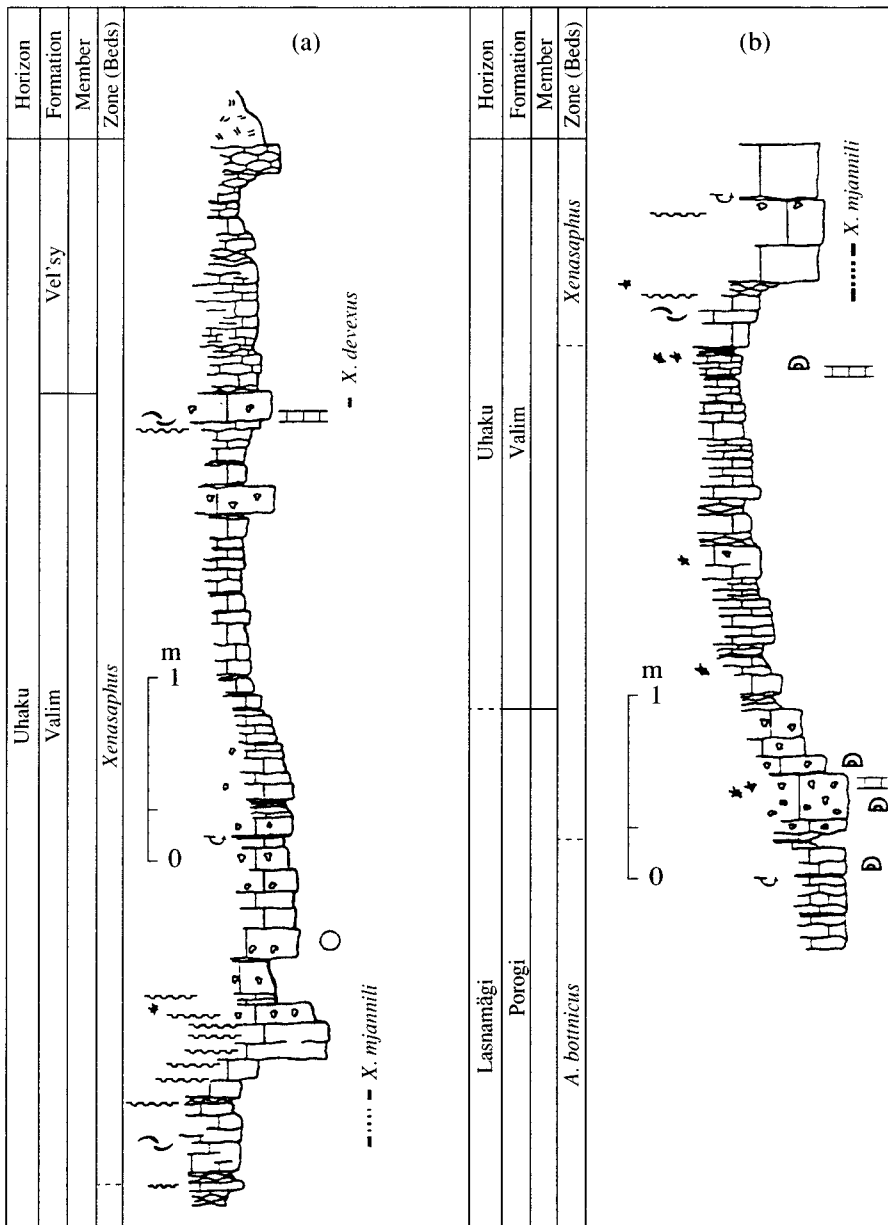
**Fig. 15.** Distribution of trilobites of the subfamily Asaphinae in the Shkurina Gorka outcrop (left bank of the Volkhov River, town of Volkhov, 0.2–1.5 km upstream of the Volkhov hydroelectric power station dam, lectostratotype of the Porogi Formation, stratotype of the beds with *A. bottnicus*; (a) upper and (b) lower parts of the outcrop). Designations as in Fig. 3.

1998). Its stratotype is situated on the left bank of the Volkhov River in the roadside of a new auto-bridge inside the boundary of the town of Volkhov.

This formation is represented by clayey limestone and marl, which are predominantly thin-laminated and lenslike, with frequent interbeds of clay. The lower boundary of the Simankovo Formation is recognized by

the appearance of heavily clayey limestone and marl in the section. This formation includes (upsection):

Member 1, which is represented by gray, lilac gray, greenish gray, lens-laminated (thin-laminated in the Volkhov hydroelectric power station dam outcrop on the Volkhov River), clayey to marl limestone with frequent interbeds of clay. The thickness is 4.7 m in the



**Fig. 16.** Distribution of trilobites of the subfamily Asaphinae in the Porogi-Valim outcrop: (a) left bank of the Volkhov River, village of Porogi, (b) same area, village of Valim. Lectostratotype of the Valim Formation, stratotype of beds with *Xenasaphus*. Designations as in Fig. 3.

stratotype and 3.7 m on the right bank of the Lava River, in an outcrop situated approximately 200 m downstream of the Kavra River mouth.

Member 2, which is represented by greenish gray, thick-laminated with poorly expressed lumpy component limestone with thin, twisting vertical traces of digging; an ill-defined discontinuity surface with the pale lilac roof of the underlying bed and rare pebbles of clayey limestone above it stretching out approximately 5 cm below the roof of the member. This surface (ds4) is traceable over the entire Ladoga Glint (Figs. 7, 12, 13) and the Leningrad part of the Baltic Glint; in the Narva

River Region, it passes into the lower surface of two approximated rusty yellow surfaces in the roof of the Napa Formation. It coincides with the margin of the *S. latisegmentatus* range and defines the lower boundary of the Aseri Horizon (Ivantsov, 1993b). The thickness of this member is around 3 m over the entire Ladoga Glint.

Member 3, which is represented by greenish gray, rosy gray, lens-laminated marl with frequent interbeds of clay. Its thickness is 2.4 m in the stratotype and around 2.25 m on the Lava River.

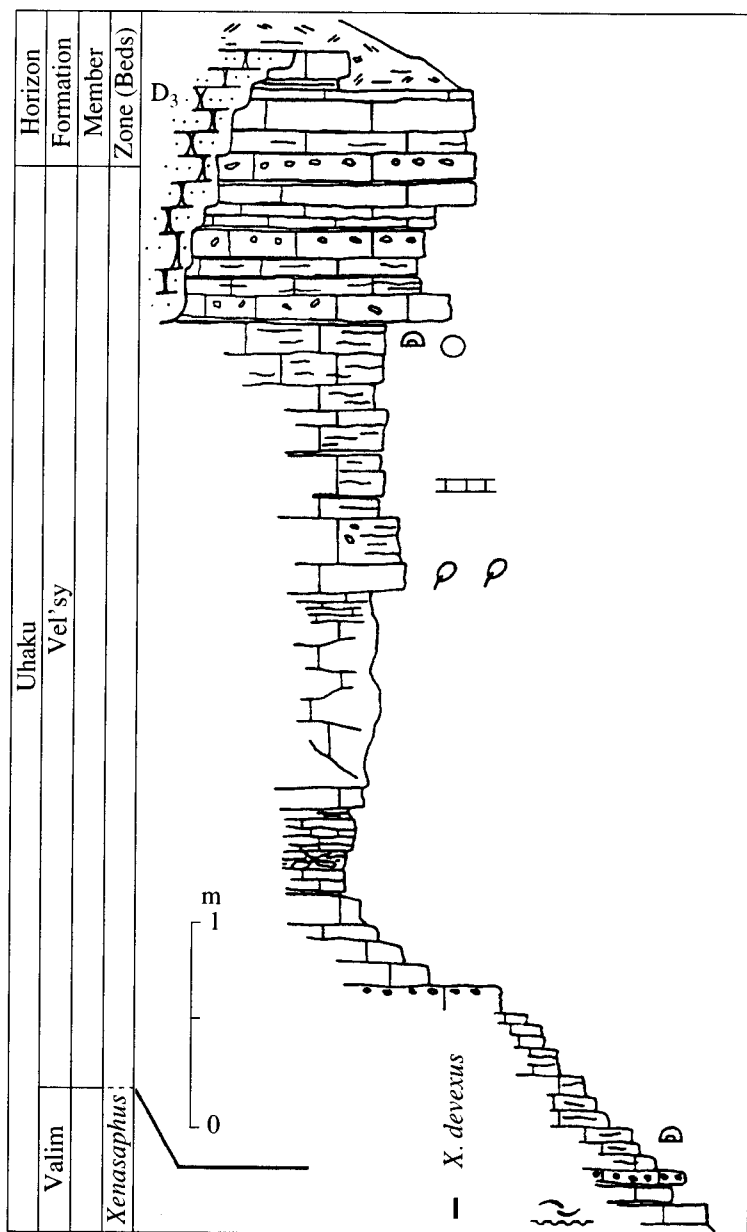


Fig. 17. Distribution of trilobites of the subfamily Asaphinae in the Bor outcrop (right bank of the Volkhov River, downstream of the railroad bridge near the village of Bor, between the bridge and the mouth of an unnamed creek). Designations as in Fig. 3.

The total thickness of the Simankovo Formation is 7.4 m in the stratotype and around 6.25 m on the Lava River. Within the Ladoga Glint, this formation is distributed everywhere. The Napa Formation and the lower part of the Aseri Formation are age analogues of this formation in the Estonian part of the Baltic Glint.

**Aseri Horizon. Duboviki Formation.** This formation was established by Raymond (1916). Its holostratotype was not designated. A section on the right bank of the Volkhov River near the village of Duboviki, immediately downstream of the Volkhov hydroelectric

power station sluice (Duboviki outcrop, Fig. 14) may be proposed as a lectostratotype.

This formation is represented by gray, rosy greenish gray, predominantly thick-laminated limestone, which ranges from clayey limestones to marls at some levels. The lithology of this formation and all superimposing Ordovician deposits of the Volkhovian section was studied in detail in the first third of the 20th century by Hecker and Yanishevskii, but their results were not published. Nonetheless, references for beds established at that time occasionally appear in the literature (Yanishevskii, 1931; Balashova and Balashov, 1961). The

lower boundary of this formation is recognized in the floor of the first thick-laminated limestone bed, which is, possibly, Hecker's Bed "c" (Ivantsov, 1993b). The thickness of this formation is 6.35 m in the lectostratotype and 7.25 m by the Lava River. This formation is distributed all over the Ladoga Glint. Within the Baltic Glint, the Aseri Formation is a synchronous analogue of this formation.

**Lasnamägi Horizon. Porogi Formation.** The name was proposed by Lesnikova and published by Balashova and Balashov (1961). The holostratotype of this formation has not been established. A section on the left bank of the Volkhov River within the boundary of the Volkhov town, 0.2–1.5 km upstream of the Volkhov hydroelectric power station Dam (Shkurina Gorka outcrop, Fig. 15) may be proposed as a lectostratotype.

This formation is represented by gray limestone, reddish in its lower part and greenish in its upper part, predominantly thick-laminated, dolomitized, and sometimes cavernous, with cavities along the fauna and iron pyrites concretions. The lower boundary of this formation was identified by Lesnikova in the floor of Hecker's Bed "k," "which is expressed as a bench in the Volkhov River sections" (Balashova and Balashov, 1961). Having found *A. ornatus*, Balashova and Balashov (1961) lowered it one bed. These samples have not been kept, but I think that there is an error, and *A. ornatus* was confused with *A. holmi*, coexisting in this bed with *A. kowalewskii*. Both the latter species are typical representatives of Aserian trilobites and are widely distributed in the deposits of the Duboviki Formation; therefore, I restore the boundary suggested by Lesnikova. In the lectostratotype, the thickness of this formation is 8.9 m. In addition to the Volkhov River, fragments of this formation are exposed along the Lava River and near the village of Putilovo. The lower part of the Vão Formation is a time analogue of this formation within the Baltic Glint.

**Uhaku Horizon. Valim Formation.** The name was proposed by Lesnikova and introduced in the literature by Balashova and Balashov (1961). The stratotype of this formation is situated in a section on the left bank of the Volkhov river near the villages of Porogi and Valim (Porogi–Valim outcrop, Fig. 16).

This formation is represented by gray clayey limestone and marl, which are spotted, of predominantly red tones, dolomitized, and occasionally cavernous. The lower boundary of this formation appeared to be recognized by Balashova in the roof of the dense limestone bed with frequent large cavities (Hecker's Bed "q" and, possibly, lower part of Bed "r"). The thickness of this formation is 6.1 m in the stratotype. Deposits of this formation are outcropped in the stratotype locality only. Within the Baltic Glint, the upper part of the Vão Formation is a time analogue of the Valim Formation.

**Vel'sy Formation.** The name was proposed by Lesnikova and published by Balashova and Balashov

(1961). The stratotype has not been defined. Outcrops near the village of Vel'sy (Vel'tsa) are submerged; Hecker's Beds "w"–"z," which were destroyed by the Early Devonian washout, are absent from other outcrops. A more or less complete section on the right bank of the Volkhov River near the village of Bor, somewhat downstream of the railway bridge, below gardens (Bor outcrop, Fig. 17) may be proposed as a lectostratotype of this formation.

The formation is represented by rosy gray dolomitized clayey limestone and marl. The lower boundary of the formation is recognized in the roof of the Bed "t," which is represented by yellowish gray dolomitized limestone with numerous *X. devexus* remains. The thickness of this formation is about 4–4.5 m in the lectostratotype. This formation outcrops nowhere else within the Ladoga Glint. Its synchronous analog within the Baltic Glint is the Kõrgella Formation.

### 1.2. Trilobite-Based Biostratigraphic Divisions of Carbonate Ordovician Deposits of the Ladoga Glint

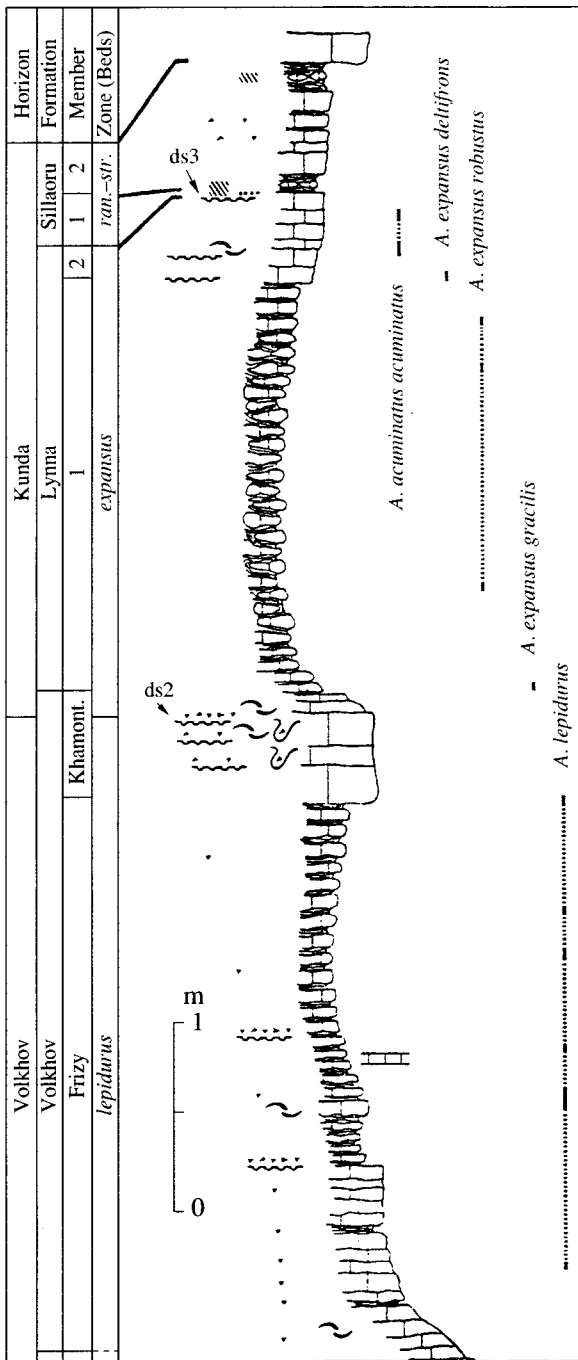
Within the Ladoga Glint section, trilobite remains occur in carbonates only. They are much diversified in the Volkhov Horizon, so the dominating group is difficult to be recognized. Asaphines and illenids begin to dominate starting from the Kunda Horizon. Illenids having a stratigraphical potential not less than asaphines have barely been studied since Schmidt's time. In the entire 20th century, only one paper was published (Jaanusson, 1954).

Since the very start of biostratigraphical studies of the Ordovician carbonates of the Baltic Region, trilobites of the genus *Asaphus* s.l. have been the main tool for sequencing them. The trilobite zones within the Glint were established by Lamanskii (1901, 1905) predominantly for the Volkhov–Kunda deposits, by Lesnikova (Yanishevskii, 1931; Balashova and Balashov, 1961) for the Aseri deposits, and by Balashova and Balashov (1959, 1961) for the Kunda–Uhaku deposits (Table 2). However, the stratigraphical distribution of trilobites was poorly studied at that time and some forms were wrongly identified. Repeated collection of material undertaken by me with assignment of samples to marking levels demonstrated that stratigraphical ranges of the majority of species were greatly overemphasized, especially in Balashova's papers. It may be explained, in addition to having a broad understanding of species, by some mistakes made by Leningrad geologists during their study of the glint sections: first, they missed several meters of the Kunda deposits in the combined section of the Volkhov River; second, they associated samples with the "upper lenticular bed" that is migration along the section and with Hecker's beds, whose volume is variously understood by various researches (Ivantsov, 1990a, 1993b).

The Kunda–Aseri part of the trilobite chart proposed in *Resheniya...* (1987) seems to be unsuccessful.

**Table 2.** Sequencing of carbonate Ordovician deposits of the Ladoga Glint on the basis of trilobites according to different authors

Lamanskii, 1901, 1905	Yanishevskii, 1931	Lesnikova (after Balashova and Balashov, 1961)	Balashova and Balashov, 1959, 1961		Resheniya..., 1987	Ivantsov, present work								
Horizon (Zone)	Horizon	Zone	Horizon	Subhorizon	Horizon	Beds	Horizon	Zone (Beds)	Other trilobites					
<i>Asaphus platyurus</i> , <i>A. kowalewskii</i> ,	<i>A. devexus</i>	<i>A. devexus</i>	Vel'sy			<i>Chasmops odini</i> , <i>Iliaenus schmidtii</i> , <i>I. intermedius</i>	Uhaku	<i>Xenasaphus</i>	<i>X. devexus</i> <i>X. njannili</i>					
										Valim	<i>A. devexus</i>	Uhaku		
	<i>Asaphus</i> sp.	<i>A. ornatus</i>	Porogi	<i>A. ornatus</i>		Lasnamägi	<i>I. shroeteri</i> , <i>A. ornatus</i>	Lasnamägi	<i>A. bottnicus</i>					
	<i>A. kowalewskii</i> , <i>A. latus</i> , <i>A. laevisimus</i> var. <i>laticauda</i>	<i>A. kowalewskii</i>	Duboviki	Volkhovstroï	<i>A. kowalewskii</i>	<i>A. cornutus</i>	<i>A. kowalewskii</i> , <i>A. cornutus</i>	Aseri	<i>A. kowalewskii</i> , <i>A. cornutus</i> , <i>A. platyurus</i>	<i>A. kowalewskii</i>	<i>A. intermedius</i>			
												<i>A. cornutus</i>	<i>A. kowalewskii</i> , <i>A. cornutus</i> , <i>A. eichwaldi</i>	Aseri
	<i>A. eichwaldi</i> , <i>Ptychopyge globifrons</i>	<i>A. eichwaldi</i>	<i>A. eichwaldi</i>	Volkhovstroï	<i>A. eichwaldi</i>	<i>A. eichwaldi</i>	<i>A. kowalewskii</i> , <i>A. cornutus</i> , <i>A. eichwaldi</i>	Kunda	<i>A. sulevi</i> , <i>P. globifrons</i> , <i>Megistaspis gigas</i> , <i>M. obtusicauda</i>	<i>A. laevisimus</i>	<i>A. ingrianus</i>			
<i>A. eichwaldi</i> , <i>A. minor</i>												<i>A. eichwaldi</i>	<i>A. pachyophthalmus</i> <i>A. minor</i>	<i>S. laticaudatus</i> <i>S. latisegmentatus</i>
												<i>A. cornutus</i> , <i>A. eichwaldi</i>	<i>A. heckeri</i>	
<i>A. raniceps</i>			Obukhovo	<i>A. major</i>		<i>A. eichwaldi</i> , <i>A. minor</i>	Kunda	<i>A. laevisimus</i>	<i>A. ingrianus</i>	<i>A. sulevi</i>	<i>A. pachyophthalmus</i> <i>A. minor</i>	<i>A. sriatus</i>	<i>P. globifrons</i> , <i>A. knyrkoi</i>	<i>I. "esmarki"</i> <i>Pliomera fischeri</i>
<i>A. expansus</i> , <i>A. lamanskii</i>				<i>A. raniceps</i>		<i>A. "raniceps"</i> , <i>M. lawrowi</i>		<i>A. laevisimus</i>	<i>A. ingrianus</i>	<i>A. sulevi</i>	<i>A. pachyophthalmus</i> <i>A. minor</i>	<i>A. sriatus</i>	<i>P. globifrons</i> , <i>A. knyrkoi</i>	
<i>A. lepidurus</i> , <i>Megalaspis gibba</i>			Volkhov	<i>A. lepidurus</i> , <i>M. gibba</i>		<i>A. lepidurus</i> , <i>M. limbata</i>	Volkhov	<i>A. lepidurus</i> , <i>M. limbata</i>	<i>A. lepidurus</i>			<i>A. lepidurus</i>		
<i>A. broeggeri</i> , <i>Onchometopus volborti</i>				<i>A. broeggeri</i> , <i>M. hyorhina</i>		<i>A. broeggeri</i>		<i>A. broeggeri</i>	<i>A. broeggeri</i>			<i>A. broeggeri</i>		
<i>A. priscus</i> , <i>M. limbata</i> , <i>M. planilimbata</i>				<i>A. priscus</i> , <i>M. limbata</i> , <i>M. planilimbata</i>		<i>M. lata</i>		<i>M. lata</i>	<i>M. polyphemus</i>			<i>M. polyphemus</i>		
						<i>M. estonica</i>		<i>M. estonica</i>						



**Fig. 18.** Distribution of trilobites of the subfamily Asaphinae in the Lynna Mouth outcrop (left bank of the Lynna River, 100–200 m upstream of its mouth, stratotype of the Lynna Formation and Khamontovo Member, lectostratotype of the beds with *A. lepidurus*). Designations as in Fig. 3. Abbreviations: (*ran.-str.*) *raniceps-striatus* Zone.

This large interval is subdivided into only four beds with trilobites; these beds are sharply unequal in their volume. Each of the two lower beds corresponds to the range of one species, whereas the upper beds corresponds to the ranges of six and five species, respectively

(Table 1). “*A. platyurus*,” which is one of the index species of the Aseri Horizon, cannot be used for detailed sequencing, for it represents a group of species ranging across the most of, or even the entire, Aseri Horizon.

The above ideas induced changes proposed by me for the trilobite chart of the Ordovician of the Eastern Baltic Region. Names of new units had been published earlier (Ivantsov and Mel’nikov, 1993; Ivantsov, 1996; 1997a, 1997b; Ivantsov and Mel’nikova, 1998), but their formal description is published here for the first time.

During recognition of zones, I preferred species presumably belonging to one phyletic line, which may help avoid a possible overlapping of the zones. There are three such lines established, *A. lepidurus*–*A. expansus*, *A. acuminatus lamanskii*–*A. pachyophthalmus*, and *A. sulevi*–*A. kowalewskii* (Fig. 23). Regrettably, a sharp impoverishment of trilobite fauna during the Middle Kundian time prevents recognition of linking chains between two latter lines; therefore, the scheme looks somewhat imperfect. A number of zones are defined by pairs of species, whose ranges are not overlapping. That has been made in the following cases: (1) when intervals of species distribution are separated by a proportional gap barren of trilobites (*raniceps-striatus* and *minor-pachyophthalmus* zones), (2) when the range of one of species is very short and, consequently, is of little use for practical stratigraphy (*sulevi-ingrianus* and *kotlukovi-punctatus* zones and beds with *A. intermedius*–*A. kowalewskii*).

At the present time, the boundaries of stratigraphical distribution of some leading forms remain unclear, deposits of the Latorp and Uhaku horizons and the lower part of the Volkhov Horizon remain unstudied. Therefore, less formal “beds with fauna” are described in the present paper alongside the zones. The distribution of asaphines in some studied sections is showed in Figs. 3–19.

**Volkhov Horizon.** The lower boundary of the horizon is recognized by the first occurrence of *M. (M.) polyphemus*. Basing on some authors’ data, it coincides with ds1 (Mägi, 1984a, 1984b; Resheniya..., 1987; Männil, 1990). Within the studied territory, the Volkhov Horizon is represented by the Volkhov Formation. This formation consists of the following beds with trilobites: (1) *M. (M.) polyphemus*, (2) *A. ? broeggeri*, (3) *A. lepidurus*. Generally, these beds nearly completely correspond to the Zone of *D. hirundo* (Resheniya..., 1987).

#### Beds with *Megistaspis (Megistaspis) polyphemus*

Horizon (Zone) of *M. limbata*, *M. planilimbata*, and *A. priscus* (BII $\alpha$ ): Lamanskii, 1901 (excluding the bottom part), 1905 (excluding the bottom part).

Zone of *A. priscus*, *M. limbata* and *M. planilimbata*: Balashova and Balashov, 1959 (excluding the bottom part).

Zone of *Productorthis obtusa* and *Paurorthis parva*, Subzone of *A. priscus*, *M. limbata*, and *M. planilimbata*: Alikhova, 1960 (excluding the bottom part).

Beds with *M. lata*: *Resheniya...*, 1987; Ivantsov and Mel'nikov, 1993.

Zone of *M. polyphemus*: Ivantsov, 1997a; Ivantsov, 1997b.

The index-species has been substituted, since *M. lata* turned out to be a junior synonym of *M. (M.) polyphemus* (Nielsen, 1995). The vertical distribution of this species in the Ladoga Glint sections has not been studied by me, and works containing a detailed analysis of megistaspid distribution within the territory under investigation are lacking. The upper part of the Dikari Member above ds1 (Saka Submember) is referred (conditionally?) to these beds (*Resheniya...*, 1987).

Beds with *A. ? broeggeri*

Horizon (Zone) of *A. broeggeri* and *O. volborthi* (BIIß): Lamanskii, 1901, 1905.

Zone of *A. broeggeri* and *Megalaspis hyorhina*: Balashova and Balashov, 1959.

Zone of *Productorthis obtusa* and *Paurorthis parva*, Subzone of *A. broeggeri* and *M. hyorhina*: Alikhova, 1960.

Beds with *A. broeggeri*: *Resheniya...*, 1987; Ivantsov and Mel'nikov, 1993; Ivantsov, 1997a; Ivantsov, 1997b.

The range of these beds is equal to a complete stratigraphical distribution of *A. ? broeggeri*. A section of the abandoned east margin of the Babino Quarry on the right bank of the Volkhov River is proposed as a type section of these beds (lectostratotype of the Volkhov Formation, the Babino outcrop, Fig. 11). In the type section, the index species appears 0.1–0.15 m above the floor of the Zheltyaki Member, or the roof of the Butok Bed (Dronov *et al.*, 1993; Dronov *et al.*, 1996). A chance of also finding it in the lower 10 cm of the member cannot be excluded, so the lower boundary of the beds is tentatively recognized in the floor of the Zheltyaki Member. Along the Baltic-Ladoga Glint, the beds are confidently traced at least to the village of Lopukhinka, in the western part of the Leningrad Region. Outside the glint, the index species is only known in the Moscow Syncline (Valdai Monocline, Volkhov Formation) (Alikhova, 1960; Dmitrovskaya, 1991).

Beds with *A. lepidurus*

Horizon (Zone) of *A. lepidurus* and *M. gibba* (BIIγ): Lamanskii, 1901, 1905.

Zone of *A. lepidurus* and *M. gibba*: Balashova and Balashov, 1959.

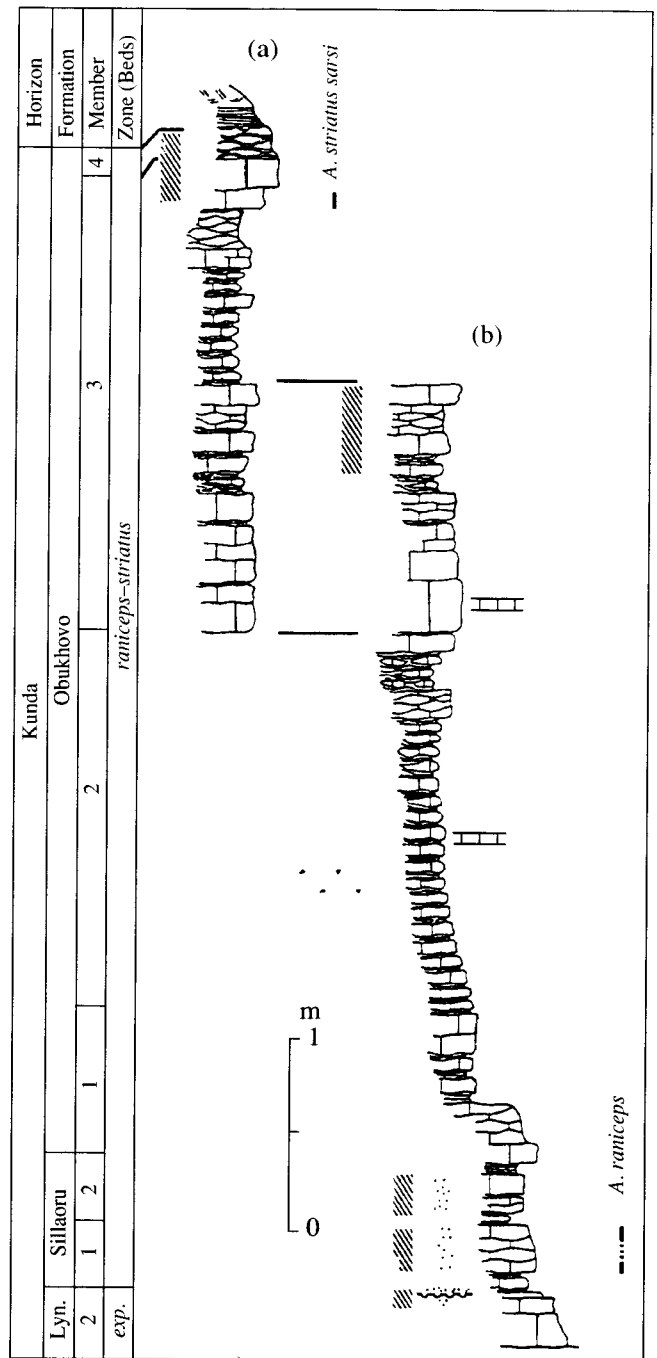


Fig. 19. Distribution of trilobites of the subfamily Asaphinae in outcrops along the Lynna River near the village of Khamontovo by the auto-bridge: (a) Khamontovo outcrop, left bank, about 700 m downstream of the bridge, (b) South Lynna outcrop, right bank, about 200 m downstream of the bridge. Designations as in Fig. 3. Abbreviations: (Lyn.) Lynna Formation, (exp.) expansus Zone.

Zone of *Productorthis obtusa* and *Paurorthis parva*, Subzone of *A. lepidurus* and *M. gibba*: Alikhova, 1960.

Beds with *Megistaspis limbata* and *A. lepidurus*: *Resheniya...*, 1987.

Beds with *A. lepidurus*: Ivantsov and Mel'nikov, 1993; Ivantsov, 1997a; Ivantsov, 1997b.

The range of these beds is equal to the complete stratigraphic range of *A. lepidurus*. An outcrop situated on the left bank of the Lynna River several meters upstream of its mouth is proposed as a type section of these beds (stratotype of the Lynna Formation, the Lynna-Mouth outcrop, Fig. 18). In this section, the index species appears 0.55 m above the floor of the Frizy Member (2.7 m beneath ds2); however, a chance of its presence in the lower beds of the member, where trilobites of the genus *Asaphus* have not been found, cannot be excluded, so the lower boundary of the beds is tentatively recognized at the floor of the Frizy Member. Within the Ladoga Glint, these beds correspond to the Frizy Member and to the lower part of the Khamontovo Member. Outside the Ladoga Glint, the beds are traced within the Baltic Glint (Toila Formation, Kalvi and Pada members, Vil'povitsy oolite lens) (Balashova, 1953, 1976; Rõõmusoks, 1960; *Resheniya...*, 1987; Ivantsov, 1990a), in the Moscow Syncline (central part, Gryazovets Formation; Valdai Monocline, Volkhov Formation) (Dmitrovskaya, 1991), in central Sweden (Männil, 1966), and in Öland Island (Bohlin, 1949).

**Kunda Horizon.** The Lower boundary of the horizon is recognized by the first occurrence of *A. expansus* (Alikhova, 1960; Männil, 1963a; *Resheniya...*, 1987, etc.). Within the Ladoga Glint, this species appears immediately above ds2 in the floor of the Sillaoru Formation ("lower lenticular bed") near the Voibokalo Station and westwards or inside the Khamontovo Member along the Volkhov and Syas' rivers. Along the Ladoga Glint, the horizon includes the following strata: the Volkhov Formation (upper part of the Khamontovo Member), the Lynna, Sillaoru, Obukhovo, Sinyavino formations, and the lower half of the Simankovo Formation. The horizon includes the following zones: (4) *A. expansus*, (5) *A. raniceps*–*A. striatus*, (6) *A. minor*–*A. pachyophthalmus*, (7) *A. sulevi*–*A. ingrianus*, (8) *A. laevissimus*. In general, the range of these zones corresponds to the upper part of the *D. hirundo* Zone and the entire *D. bifidus* Zone (*Resheniya...*, 1987).

#### Zone of *A. expansus*

Horizon (Zone) of *A. expansus* and *A. lamanskii* (BIII $\alpha$ ): Lamanskii, 1901, 1905.

Zone of *A. expansus* and *A. lamanskii*: Balashova and Balashov, 1959.

Zone of *Lycophoria nucella* and *Endoceras incognitum*, Subzone of *A. expansus* and *A. lamanskii*: Alikhova, 1960.

Beds with *A. expansus*: *Resheniya...*, 1987; Ivantsov and Mel'nikov, 1993; Ivantsov, 1996.

Zone of *A. expansus*: Ivantsov, 1997a; Ivantsov, 1997b.

The range of these beds is equal to the complete stratigraphic range of *A. expansus*, which corresponds to the upper quarter of the *D. hirundo* Zone (*Resheniya...*, 1987). An outcrop situated on the right bank of the Volkhov River in an abandoned quarry approximately 1 km upstream of the village of Obukhovo is proposed as a type section of this zone. The index species appears immediately above ds2 in all sections. The zone corresponds to the upper half of the Khamontovo Member of the Volkhov Formation and Lynna Formation in the sections along the Volkhov and Syas' rivers and to the Nikol'skoe Member of the Sillaoru Formation in the sections of the Voibokalo Station, the Lava River, the village of Putilovo and farther along the glint to the village of Toila in Estonia, at least. This zone is traced in the Moscow Syncline (Veksino Formation in the central part and Obukhovo Formation in the Valdai Monocline), in southern Estonia and western Latvia (Shakino Formation (*Resheniya...*, 1987; Ulst *et al.*, 1984) and the Baldon Formation (?) (Ulst *et al.*, 1984)), in central Sweden (lower part of the Hulen Limestone (*Resheniya...*, 1987; Bohlin, 1949)), and Norway (Oslo graben, *Orthoceras* Limestone 3c<sup>Byr</sup> (Männil, 1966)).

#### Zone of *A. raniceps* and *A. striatus*

Horizon (Zone) of *A. raniceps* (BIII $\beta$ ): Lamanskii, 1901, 1905.

Horizon (Zone) of *A. eichwaldi* and *P. globifrons*: Lamanskii, 1901 (lower part); 1905 (lower part).

Zone of *A. raniceps*: Balashova and Balashov, 1959.

Zone of *A. major* and *Cyclendoceras cancellatum*: Balashova and Balashov, 1959.

Zone of *Lycophoria nucella* and *Endoceras incognitum*, Subzone of *A. raniceps*: Alikhova, 1960.

Zone of *Lycophoria nucella* and *Endoceras incognitum*, Subzone of *C. cancellatum* and *A. major*: Alikhova, 1960.

Beds with *A. "raniceps"* and *Megistaspis lawrovi*: *Resheniya...*, 1987.

Beds with *A. sulevi*, *M. gigas*, *M. obtusicauda*, and *Pseudasaphus globifrons*: *Resheniya...*, 1987 (lower part).

Beds with *A. "raniceps"*: Ivantsov and Mel'nikov, 1993.

Beds with *A. knyrkoi* and *A. pachyophthalmus*: Ivantsov and Mel'nikov, 1993 (lower part).

Beds with *A. "raniceps"* and *A. striatus*: Ivantsov, 1996.

Zone of *A. "raniceps"* and *A. striatus*: Ivantsov, 1997a; Ivantsov, 1997b.

The range of this zone is equal to the stratigraphical intervals of *A. raniceps* and *A. striatus* combined. An outcrop on the left bank of the Volkhov River below the village of Zvanka (lectostratotype of the Obukhovo

Formation, the Zvanka outcrop, Fig. 12) is proposed as the type section of this zone. The lower boundary of this zone is recognized by the first occurrence of *A. raniceps* 0.15 m above ds3 in the stratotype and immediately above this surface in sections westward of the stratotype, and apparently coincides with ds3. This zone corresponds to the upper member of the Sillaoru Formation and the entire Obukhovo Formation. The zone is well-traced along the Ladoga Glint and is traced with difficulty (due to the nearly complete absence of trilobite remains) along the Narva River within the Baltic Glint, where it corresponds to the Utria Formation and the lower part of the Valgejõe Member of the Loobu Formation. *Asaphus "raniceps"* is often mentioned in stratigraphical literature; however, judging from the wide interval of its stratigraphical distribution, this name covers the full range of forms from *A. acuminatus lamanskii* to *A. striatus striatus*. *A. raniceps* s.l. is known from the western part of the Baltic Glint (Nõmmeveski Member of the Loobu Formation (Rõõmusoks, 1960) and Suurupi Member of the Pakri Formation (*Resheniya...*, 1987)), from the Moscow Syncline (Veksino Formation in the central part and Obukhovo Formation in the Valdai Monocline (Dmitrovskaya, 1989; 1991)), from western Latvia and western Lithuania (Shakino Formation (*Resheniya...*, 1987), from the Baldone Formation and Šupili Member (Ulst *et al.*, 1984)), from southeastern Latvia and eastern Lithuania (Bičiunai and Juodupe formations, Mikona and Obyalskaya members, the lower part of Rokiškis Formation (Lashkov *et al.*, 1984; *Resheniya...*, 1987), from north-western Belarus (the upper part of the Pivori Formation and the Tviariačius Formation (Lashkov *et al.*, 1983; *Resheniya...*, 1987)), from Öland Island (middle part of the Hulen Limestone (Bohlin, 1949, 1955)), and from northeastern Poland (Modlinski and Pokorski, 1964). Except for the east part of the Baltic-Ladoga Glint, *A. striatus* is known from the type locality only (Norway, Oslo graben, *Orthoceras* Limestone 3c<sup>γ</sup> (Störmer, 1940, 1953; Wandäs, 1983)).

#### Zone of *A. minor* and *A. pachyophthalmus*

Horizon (Zone) of *A. eichwaldi* and *P. globifrons* (BIII<sup>γ</sup>): Lamanskii, 1901 (partly), 1905 (partly).

Horizon with *A. eichwaldi*, *A. laevisimus*, and *A. cornutus*: Yanishevskii, 1931 (lower part).

Zone of *Christiania oblonga* and *Orthoceras regulare*, Subzone of *A. cornutus*, *A. kowalewskii*, and *A. eichwaldi*: Alikhova, 1960 (partly).

Zone of *A. eichwaldi*, Subzone of *A. eichwaldi* and *A. minor* (C1<sup>α</sup>): Balashova and Balashov, 1961.

Beds with *A. sulevi*, *Megistaspis gigas*, *M. obtusicauda*, and *Pseudasaphus globifrons*: *Resheniya...*, 1987 (middle part).

Beds with *A. knyrkoi* and *A. pachyophthalmus*: Ivantsov and Mel'nikov, 1993 (upper part).

Beds with *A. minor* and *A. pachyophthalmus*: Ivantsov, 1996.

Zone of *A. minor* and *A. pachyophthalmus*: Ivantsov, 1997a; Ivantsov, 1997b.

The range of this zone is equal to the stratigraphical intervals of *A. minor* and *A. pachyophthalmus* combined. A section on the left bank of the Volkhov River between of the Volkhov hydroelectric power station dam and the northern outskirts of the village of Zvanka is proposed as a type section of the zone (Figs. 12, 13). The lower boundary of this zone is recognized by the first occurrence of *A. minor*. The range of this species is 0.05 m below to 0.4 above the Sinyavino Formation floor in the type section, which is 4.7–5.15 m below ds4, or from 0.4 m below to 0.8 m above the Sinyavino Formation floor in the Putilovo Quarry section, which is 4–5.8 m above ds3. Thus, this zone corresponds to the upper part of Member 4 of the Obukhovo Formation, Sinyavino Formation, and the lower part of Member 1 of the Simankovo Formation. This zone is badly traced outside of the Ladoga Glint due to a nearly complete absence of trilobite remains at this level. Isolated records of the index species are known in the Baltic Glint (upper part of the Valgejõe Member of the Loobu Formation and Napa Formation (Balashova, 1953; 1976; Rõõmusoks, 1960)), in the Moscow Syncline (Gryazovets Depression and the upper half of the Kunda Horizon (Alikhova, 1960)), and in northeastern Poland (Modlinski and Pokorski, 1964).

#### Zone of *A. sulevi* and *A. ingrianus*

Horizon (Zone) of *A. eichwaldi* and *P. globifrons* (BIII<sup>γ</sup>): Lamanskii, 1901 (partly), 1905 (partly).

Horizon with *A. eichwaldi*, *A. laevisimus*, and *A. cornutus*: Yanishevskii, 1931 (middle part).

Zone of *Christiania oblonga* and *Orthoceras regulare*, Subzone of *A. cornutus*, *A. kowalewskii*, and *A. eichwaldi*: Alikhova, 1960 (partly).

Zones *A. eichwaldi* and *A. cornutus*, Subzone of *A. cornutus* and *A. eichwaldi* (C1<sup>α</sup>): Balashova and Balashov, 1961 (lower part).

Beds with *A. sulevi*, *Megistaspis gigas*, *M. obtusicauda*, and *Pseudasaphus globifrons*, *Resheniya...*, 1987 (middle part).

Beds with *A. "sulevi"*: Ivantsov and Mel'nikov, 1993.

Beds with *A. sulevi* and *A. ingrianus*: Ivantsov, 1996.

Zone of *A. sulevi* and *A. ingrianus*: Ivantsov, 1997a; Ivantsov, 1997b.

The range of this zone is equal to the stratigraphical intervals of *A. sulevi* and *A. ingrianus*, which are connected by direct relationship. A section on the left bank of the Volkhov River between the Volkhov hydroelec-

tric power station dam and the railway bridge (the Volkhov hydroelectric power station dam outcrop, Fig. 13) is proposed as a type section of this zone. The lower boundary of the zone is recognized by the first occurrence of *A. sulevi*, which happens in the upper part of Member 1 of the Simankovo Formation in the type section, i.e., 1.4 m below ds4. Within the Ladoga Glint, this zone corresponds to the upper part of Member 1 of the Simankovo Formation only. The zone is traced in the Baltic Glint, where it correlates with the middle part of the Napa Formation (Balashova, 1953, 1976; Rõõmusoks, 1960), on Öland Island, where it correlates with the middle part of the Hulen Limestone, beds with *M. obtusicanda* (Bohlin, 1955), and in northeastern Poland (Modlinski, 1973).

#### Zone of *A. laevissimus*

Horizon (Zone) of *A. eichwaldi* and *P. globifrons* (BIIIy): Lamanskii, 1901 (upper part), 1905 (upper part).

Horizon with *A. eichwaldi*, *A. laevissimus*, and *A. cornutus*: Yanishevskii, 1931 (middle part).

Zone of *Christiania oblonga* and *Orthoceras regulare*, Subzone of *A. cornutus*, *A. kowalewskii*, and *A. eichwaldi*: Alikhova, 1960 (partly).

Zones *A. eichwaldi* and *A. cornutus*, Subzone of *A. cornutus* and *A. eichwaldi* (C1 $\alpha$ ): Balashova and Balashov, 1961 (upper part).

Beds with *A. sulevi*, *Megistaspis gigas*, *M. obtusicanda*, and *Pseudasaphus globifrons*: Resheniya..., 1987 (upper part).

Beds with *A. laevissimus*: Ivantsov and Mel'nikov, 1993; Ivantsov, 1996.

Zone of *A. laevissimus*: Ivantsov, 1997a; Ivantsov, 1997b.

The range of this zone is equal to the stratigraphical range of *A. laevissimus*. A section on the left bank of the Volkhov River between the Volkhov hydroelectric power station dam and the railway bridge (the Volkhov hydroelectric power station dam outcrop, Fig. 13) is proposed as a type section of this zone. The lower boundary of the zone is recognized by the occurrence of the index species, which appears 0.35 m below ds4 in the type section. Within the Ladoga Glint, this zone corresponds to the lower part of Member 2 of the Simankovo Formation up to ds4. This zone is easily traced in all sections of the Baltic-Ladoga Glint to the Narva River at least, where remains of *A. laevissimus* are found in the upper 0.1 m of the Napa Formation (Ivantsov, 1993b). Finds of the index species are also known from the Estonian part of the Baltic Glint (Balashova, 1976; Rõõmusoks, 1960), from the northern slope of the Belorussian massif (Lashkov *et al.*, 1983), and from northeastern Poland (Modlinski, 1973).

**Aseri Horizon.** *A. platyurus* is usually accepted as a characteristic fossil of the lower part of the horizon (Männil, 1963a, 1963b); 1966; Resheniya..., 1987).

However, as has been mentioned above, this species is understood in a very broad sense. The neotype of *S. platyurus* that came from Öland Island (Jaanusson, 1953b) differs considerably from the Ladoga representatives of this genus with *S. latisegmentatus* being distributed in the base of the Aseri Horizon and *S. spinifer* being distributed in its middle part. Judging from specimens discovered by amateur collectors, *Subasaphus* individuals possessing genal spines (= *A. platyurus* s. l.) do occur upsection as well. Thus, the range of *A. platyurus* s. l. comprises the entire Aseri Horizon. *A. heckeri* stays between *A. laevissimus* and *A. kotlukovi* on the basis of its morphological features, and filling an adequate position in the row of zonal forms may characterize this zone. Frankly, trilobite remains have only been found within the Baltic-Ladoga Glint so far. Possibly, during identification this species is confused with *A. laevissimus* and *Subasaphus*, which it resembles, and its range of distribution is wider. *A. heckeri* appears within the first centimeters above ds4; therefore, this surface may be accepted as the lower boundary of the horizon. In the Ladoga Glint sections, the horizon is composed of the upper half of the Simankovo Formation and Duboviki Formation. This horizon includes the following zones: (9) *A. heckeri*, (10) *A. kotlukovi* and *A. punctatus*, and (11) beds with *A. intermedius* and *A. kowalewskii*. In general, the horizon corresponds to the lower half of the *D. purchisoni* Zone (Resheniya..., 1987).

*A. platyurus* s. l. is very widely distributed. Outside the Ladoga Glint, it has been found on the Baltic Glint in the lower part of the Duboviki Formation and in the Mallas Member of the Aseri Formation (Balashova, 1953, 1976; Rõõmusoks, 1960; Resheniya..., 1987), in western and southeastern Latvia and in western and eastern Lithuania (Alikhova, 1960; Gailite, 1978; Männil, 1963a, 1966; Sverzhinskii, 1971) in the Segerstad Formation (Ulst *et al.*, 1984; Resheniya..., 1987) and in the Vajdleni Member of the Rokiškis Formation (Lashkov *et al.*, 1984), in central Sweden, on Öland Island, near Siljan Lake and in Västergötland in the Segerstad Limestone (Bohlin, 1949; Jaanusson, 1953b, 1963, 1964), in Norway (Oslo graben) (Männil, 1966), in northeastern Poland (Modlinski and Pokorski, 1964), and, possibly, on Novaya Zemlya (Bondarev, 1960).

#### Zone of *A. heckeri*

Horizon with *A. platyurus* and *A. kowalewskii*: Lamanskii, 1901.

Horizon with *A. eichwaldi*, *A. laevissimus*, and *A. cornutus*: Yanishevskii, 1931 (upper part).

Zone of *Christiania oblonga* and *Orthoceras regulare*, Subzone of *A. cornutus*, *A. kowalewskii*, and *A. eichwaldi*: Alikhova, 1960 (partly).

Zones of *A. eichwaldi*-*A. kowalewskii*, Subzone of *A. kowalewskii*, *A. cornutus* and *A. eichwaldi* (C1 $\alpha$ ): Balashova and Balashov, 1961 (partly).

Beds with *A. kowalewskii*, *A. cornutus*, and *A. platyurus*: *Resheniya...*, 1987 (lower part).

Beds with *A. platyurus* and *A. laticaudatus*: Ivantsov and Mel'nikov, 1993.

Beds with *A. platyurus*: Ivantsov, 1996.

Zone of *A. latisegmentatus*: Ivantsov, 1997a; Ivantsov, 1997b.

The volume of this zone is equal to the range of *A. heckeri*. The lower boundary of the zone is defined by the first occurrence of this species, which is recorded immediately above the fourth discontinuity surface. Within the Ladoga Glint, this zone corresponds to the upper part of Member 2 and Member 3 of the Simankovo Formation excluding its upper portion. A section on the left bank of the Volkhov River between the Volkhov hydroelectric power station dam and the railway bridge (Volkhov hydroelectric power station dam outcrop, Fig. 13) is proposed as a type section of the zone.

Zone of *A. kotlukovi* and *A. punctatus*

Horizon with *A. cornutus*: Yanishevskii, 1931.

Zone of *Christiania oblonga* and *Orthoceras regulare*, Subzone of *A. cornutus*, *A. kowalewskii*, and *A. eichwaldi*: Alikhova, 1960 (partly).

Zones of *A. eichwaldi*–*A. kowalewskii*, Subzone of *A. kowalewskii*, *A. cornutus*, and *A. eichwaldi* (C1 $\alpha$ ): Balashova and Balashov, 1961 (upper part).

Zones of *A. cornutus* and *A. kowalewskii*, Subzone of *A. kowalewskii* and *A. cornutus* (C1 $\alpha$ ): Balashova and Balashov, 1961 (lower part).

Beds with *A. kowalewskii*, *A. cornutus*, and *A. platyurus*, *Resheniya...*, 1987 (middle part).

Beds with *A. "cornutus"*: Ivantsov and Mel'nikov, 1993.

Beds with *A. kotlukovi* and *A. punctatus*: Ivantsov, 1996.

Zone of *A. kotlukovi* and *A. punctatus*: Ivantsov, 1997a; Ivantsov, 1997b.

The volume of this zone is equal to the combined ranges of *A. kotlukovi* and *A. punctatus*, which are linked by a direct relationship. A section on the left bank of the Volkhov River between the Volkhov hydroelectric power station dam and the railway bridge (Volkhov hydroelectric power station dam outcrop, Fig. 13) is proposed as a type section of the zone, the lower boundary of the zone is recognized by the first occurrence of *A. kotlukovi* that happens in the upper part of Member 3 of the Simankovo Formation, 1.55 m above ds4 in the type section. Within the Ladoga Glint, this zone corresponds to the upper part of Member 3 of the Simankovo Formation and the lower part of the Duboviki Formation. The zone is traced within the Baltic Glint, where it correlates with the middle portion of the Duboviki Formation and the Mallas Member of the

Aseri Formation (Balashova, 1953, 1976; *Resheniya...*, 1987). *A. punctatus* is also known in northwestern Belorussia, from the lower half of the Miory Formation (Lashkov *et al.*, 1983).

Beds with *A. intermedius* and *A. kowalewskii*

Horizons with *A. latus*, *A. kowalewskii*, *A. cornutus* var., and *A. laevissimus* var. *laticauda*: Yanishevskii, 1931.

Zone of *Christiania oblonga* and *Orthoceras regulare*, Subzone of *A. cornutus*, *A. kowalewskii*, and *A. eichwaldi*: Alikhova, 1960 (upper part).

Zones *A. cornutus* and *A. kowalewskii*, Subzone of *A. kowalewskii* and *A. cornutus* (C1 $\alpha$ ): Balashova and Balashov, 1961 (upper part).

Zone of *A. kowalewskii*, Subzone of *A. kowalewskii* (C1 $\alpha$ ): Balashova and Balashov, 1961.

Beds with *A. kowalewskii*, *A. cornutus*, and *A. platyurus*: *Resheniya...*, 1987 (upper third).

Beds with *A. "kowalewskii"*: Ivantsov and Mel'nikov, 1993.

Beds with *A. intermedius* and *A. kowalewskii*: Ivantsov, 1996, 1997; Ivantsov, 1997a.

The beds are equal to stratigraphical ranges of *A. intermedius* and *A. kowalewskii*. A section on the right bank of the Volkhov River 50 m downstream of the Volkhov hydroelectric power station sluice (lectostratotype of the Duboviki Formation, Duboviki outcrop, Fig. 14) is proposed as a type section of these beds. The lower boundary is defined by the first occurrence of *A. intermedius* that occurs in the middle part of the Duboviki Formation, 4.45 m above ds4 in the type section. Within the Ladoga Glint, these beds incorporate the upper half of the Duboviki Formation. The beds are traced on the Baltic Glint, where they correspond to the upper part of the Duboviki Formation and the Ojaküla Member of the Aseri Formation (Balashova, 1953, 1976; *Resheniya...*, 1987; Rõõmusoks, 1960), in the Moscow Syncline (Valdai Monocline, Polomet' Formation (Alikhova, 1960; Dmitrovskaya, 1991; Selivanova, 1971)), and in northeastern Poland (Pomorze Beds (Bednarczik, 1966)).

**Lasnamägi Horizon.** The boundary between the Lasnamägi and Uhaku horizons is recognized with difficulty on the basis of trilobites due to the rarity and fragmentary preservation of their remains. Mentioned in *Resheniya...* (1987) beds with *A. ornatus* (= *A. bottnicus* + *A. ? ornatus*) appear to correspond to the upper half of the Porogi Formation only. Trilobite remains occasionally occurring in the lower part of this formation are hardly identifiable. Therefore, in the Ladoga Glint sections, the lower boundary of the Lasnamägi Horizon is tentatively established in the floor of the Porogi Formation, immediately below which the last representatives of *A. kowalewskii* are disappearing. The biostratigraphical volume of the horizon is equal to the

upper half of the *D. purchisoni* Zone (*Resheniya...*, 1987). In the rear part of the Ladoga Glint, the horizon is entirely represented by the Porogi Formation (*Resheniya...*, 1987). The horizon includes (12) beds with *A. bottnicus*.

#### Beds with *A. bottnicus*

Zone of *Christiania oblonga* and *Orthoceras regulare*, Subzone of *A. ornatus*: Alikhova, 1960.

Zone of *A. ornatus* (C1β): Balashova and Balashov, 1961.

Beds with *A. ornatus* and *Illaeus schroeteri*: *Resheniya...*, 1987.

Beds with *A. bottnicus*: Ivantsov, 1997a; Ivantsov, 1997b.

These beds correspond to the complete range of *A. bottnicus* (= *A. ornatus* Pompecki sensu Schmidt (part) (Schmidt, 1901)). A section on the left bank of the Volkhov River 0.2–1.5 m upstream of the Volkhov hydroelectric power station dam (lectostratotype of the Porogi Formation, Shkurina Gorka outcrop, Fig. 15). The lower boundary of these beds is recognized by the first occurrence of the index species, which happens in the middle part of the Porogi Formation, approximately 4.5 m above its floor in the type section. A gap of about 5 m nearly barren of trilobite remains is observable between the beds with *A. bottnicus* and the beds with *A. intermedius* and *A. kowalewskii*. In addition to the stratotype location, these beds are traced along the Lava River, and outside the Ladoga Glint, in Sweden (Southern Botnic Region, Öland Island, Siljan Lake Region, and Furudal Limestone) and in Norway (Oslo graben) (Henningsmoen, 1960; Jaanusson, 1953b). Finds of "*A. ornatus*" were recorded within the Baltic Glint (Tallinn, apparently the Vao Formation (Balashova, 1976)) and in the Moscow Syncline (Valdai Monocline, Polomet' Formation (Alikhova, 1960; Dmitrovskaya, 1991)).

**Uhaku Horizon.** The lower boundary of the horizon is tentatively established at the Valim Formation floor, since the fauna of this horizon is poorly investigated. In the rear part of the Ladoga Glint, this horizon is composed of the Valim and Vel'sy formations (*Resheniya...*, 1987). Within the Ladoga Glint, this horizon is represented by beds, in general corresponding to the *G. teretiusculus* Zone (*Resheniya...*, 1987): (13) beds with *Xenasaphus* and (14) beds with *Chasmops odini*, *Illaeus intermedius*, and *I. schmidti*.

#### Beds with *Xenasaphus*

Zone of *Christiania oblonga* and *Orthoceras regulare*, Subzone of *A. devexus* and *Ancistroceras undulata*: Alikhova, 1960.

Zone of *A. devexus* (C1γ): Balashova and Balashov, 1961.

Beds with *Xenasaphus devexus*: *Resheniya...*, 1987.

Beds with *X. (Xenasaphus)*: Ivantsov, 1997a.

These beds correspond to the stratigraphical interval with the maximal occurrence of trilobites of the genus *Xenasaphus* (= *Asaphus devexus* sensu Schmidt (partly) (Schmidt, 1901)) and correlate with the lower part of the *G. teretiusculus* Zone. An outcrop on the left bank of the Volkhov River near the village of Valim (lectostratotype of the Valim Formation, Porogi–Valim outcrop, Fig. 16) is proposed as a type section of these beds. The lower boundary of these beds is recognized by the floor of the first mass occurrence of *X. mjannili*, which is 2 m above the Valim Formation floor. The upper boundary of these beds is recognized by the last mass occurrence of *X. devexus*, which is 6 m above the floor of the Valim Formation in the type section. Within the Ladoga Glint, these beds include the upper part of the Valim Formation. Representatives of the subgenus occasionally occur in the underlying deposits of the Porogi Formation of the Lasnamägi Horizon [a single unidentifiable specimen (Pl. 20, fig. 8) has been found in the section of the Volkhov River, 5.1 m above the Porogi Formation floor in association with *A. bottnicus*]. In addition to the Volkhov River section, trilobite remains have been found in some points of the Baltic Glint (Balashova, 1953, 1976; Schmidt, 1901), in the Moscow Syncline (central part, Luna Formation (Dmitrovskaya, 1991)), and in the Valdai Monocline (Polomet' Formation (Alikhova, 1960; Balashova, 1976; Dmitrovskaya, 1989, 1991)).

Beds with *Chasmops odini*, *Illaeus intermedius*, and *I. schmidti*

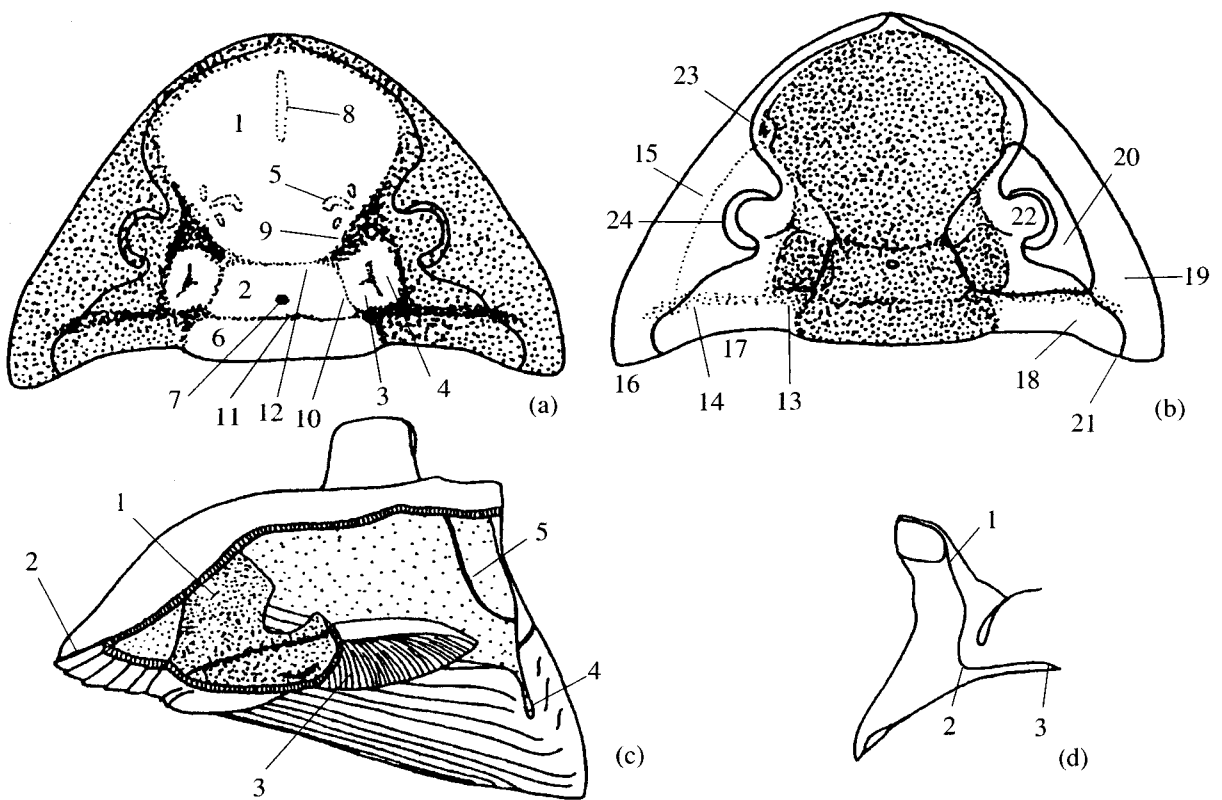
Beds with *Chasmops odini*, *Illaeus intermedius*, and *I. schmidti*: *Resheniya...*, 1987.

These beds are tentatively correlated to the Vel'sy Formation (*Resheniya...*, 1987). The distribution of the index species in sections has not been studied in detail.

Superimposing Ordovician horizons appear not to be outcropped in the Ladoga Glint Region.

## 2. PALEONTOLOGY

The trilobites of the genus *Asaphus* (in this paper, *Asaphinae*) from the Ladoga part of the glint have been known to the early researchers of the Ordovician fauna of the Baltic region, but they have been never studied separately from the fauna of the Baltic part of the glint. New species of *Asaphinae* of the Volkhov–Uhakian time were described in these regions by Pander (1830), Eichwald (1840), Lawrow (1856), Nieszkowskii (1859), Schmidt (1898, 1901), Lamanskii (1905), Lesnikova (Lesnikova and Weber, 1949), Jaanusson (1953a, 1953b), Balashova (1953, 1976), and the author (Ivantsov, 2000). Only in the Ladoga Glint,



**Fig. 20.** Structure of the trilobite cephalon in the subfamily Asaphinae: (a) rachis area (pale): (1–5) glabella lobes: (1) frontal, (2) medial, (3, 4) basal: (3) glabellar, (4) genal composite, (5) rudimentary lobes, (6) occipital ring, (7) medial (occipital) tubercle, (8) keel-like ridge, (9–11) furrows: (9) glabellar, (10) pseudodorsal, (11) occipital, (12) transverse flexure of glabella; (b) pleural area (pale): (13–15) furrows: (13) dorsal, (14) posterior marginal, (15) paradoublural, (16, 17) genae: (16) librigena, (17) fixed gena, (18) posterior marginal bordering, (19) lateral portion of gena, (20) ocular area (outlined), (21) facial suture, (22) ocular ridge, (23) fossula, (24) watching surface of eye; (c) scheme of attaching hypostome to cephalon: (1) anterior flange of hypostome, (2) anterior branch of facial suture, (3) wedgelike process of hypostomal bordering, (4) panderian organs, (5) posterior branch of facial suture (inner surface of carapace is dotted); (d) bends of anterior branch of facial suture: (1) ocular, (2) marginal, (3) anterior.

Schmidt (1901) met *A. raniceps* var. *lamanskii* ... Balashova (1976) removed from this list *A. ingrianus* and *A. devexus*. To my knowledge only *A. knyrkoi* and *X. mjannili* and (of new taxa) *A. minutus* and *A. expansus gracilis* are restricted to this area.

### 2.1. The Morphology of Trilobites of the Subfamily Asaphinae

The structure of the carapace of asaphine trilobites differs remarkably from the generalized scheme published in manuals (*Slovar'*..., 1982; *Treatise*..., 1959). It forces us to consider the general morphology of Asaphinae. Terms, which have not been used in the Russian literature, as well as new terms and those with changed meaning have asterisks; descriptions of individual morphological elements are accompanied with references to specimens, which demonstrate these characters clearly.

The cephalon of asaphine is rounded triangular (Fig. 20a), shortened (Pl. 1, fig. 1b) to elongated (Pl. 15, fig. 6a), rounded anteriorly (Pl. 6, fig. 2a) or acuminate

(Pl. 3, fig. 3a). The anterior margin of the cephalon is horizontal (Pl. 2, fig. 1d), but more often is bent beaklike (Pl. 3, fig. 5b). The glabella is divided by a shallow flexure into a large frontal\* lobe, which is pear-shaped (Pl. 7, fig. 3a) or rhomboid (Pl. 19, fig. 1a), and a small trapezoid medial\* lobe. The frontal\* lobe is convex, not reaching the anterior margin (Pl. 3, fig. 3a), reaching it (Pl. 2, fig. 3), or rarely overhanging it (Pl. 7, fig. 3e). The dorsal furrows are more or less distinct on the frontal lobe and shallow and often unnoticeable on the occipital part of the glabella. There is only one pair of glabellar furrows, extending to the occipital furrow and separating from the glabella small areas usually called the basal lobes. However, the term "basal lobes of the glabella" is not fully correct, for each of them is formed by the fusion of one, maybe two, glabellar lobes referring to the rachial part of the shield and the genal lobe belonging to the pleural part of the shield. The twofold structure of the basal lobes is sometimes visible in casts and, in some species, on the outer surface of the carapace as well (Pl. 1, figs. 1b, 3a). Usually, the genal component is more strongly developed, and the

basal lobe is lenslike (Pl. 11, fig. 1a); rarer, it is trapezoid, if both parts are equally developed (Pl. 1, fig. 1). Unlike the anterior section, the posterior section of the glabellar furrow is bent parallel to the lateral margin of the glabella. It is usually shallower than the anterior section but is deeper than the occipital portion of the dorsal furrow, suppresses and substitutes the latter, forming the pseudodorsal\* furrow. In rare cases, the glabella is not divided into lobes (Pl. 19, fig. 5a). Two to three pairs of elongated tubercles, which are possibly rudiments of the anterior lobes of the glabella, are occasionally developed on the lateral margins of the frontal\* lobe near the glabellar lobes. These rudimentary lobes\* are best visible in casts, but are sometimes expressed on the outer surface of the carapace, more often in species close to *A. raniceps* (Pl. 21, fig. 11). A keel-like ridge\* stretched along the glabellar axis (Pl. 15, fig. 1b) or a shallow pit (Pl. 2, fig. 4a) is observed in the anterior part of the frontal lobe\* in some species. The medial lobe\* usually has a medial (occipital) node\* (Pl. 3, fig. 4a). The fossulae\* are usually present and expressed as more or less diffused depressions limiting anteriorly the dorsal furrows (Pl. 16, fig. 8). The occipital furrow may be developed for the entire width of the rachis (Pl. 1, fig. 1), or developed as an isolated pit (Pl. 9, fig. 4a), or absent (Pl. 16, fig. 1). The occipital ring is flat (Pl. 15, fig. 6a; Pl. 21, fig. 3) or convex (Pl. 2, fig. 3a, 4c).

The pleural part of the shield (Fig. 20b) is divided by the paradoublure and posterior marginal furrows into the ocular area\*, lateral part of the gena and posterior marginal bordering. Since the dorsal furrows are usually weakly developed near the eyes and are replaced by the pseudodorsal\* furrows, the basal lobes turn out to be included into the ocular areas\*. In several species, the ocular area is developed as an elevation (Pl. 10, fig. 4b). A tubercle may be developed in the posterolateral corner of the ocular area (Pl. 10, fig. 3a), and a weakly expressed crestlike ridge extends along the posterior margin of *A. ? broeggeri* (Pl. 16, fig. 1), this ridge draws the latter species nearer to representatives of the family Ptychopygidae. In some forms, an elongated swelling, which may be an analogue of the eye list\* of other trilobites, extends from the eye toward the rudimentary lobes\* (Pl. 9, fig. 3b). The facial suture divides the pleural component of the cephalon into the librigena (movable cheek) and fixed gena. The anterior branch of the facial suture has several bends (Fig. 20d), the ocular\* bend is situated on the anterior side of the eye (Pl. 11, fig. 4b), the marginal\* bend is situated near the anterior margin of the shield, and the anterior\* one is expressed on the anterior margin of the shield. The marginal bend may be rounded (Pl. 6, fig. 4b) or angular (Pl. 10, fig. 7). Depending on the expression of the anterior bends, the cranidium may be obtuse (Pl. 2, fig. 4b), acuminate (Pl. 6, fig. 4b), or possessing a more or less developed lingula (Pl. 3, fig. 1b). The distance between the anterior branches of the facial sutures at the level of the marginal bends is greater than such distance at the eye socle (except for species with developed eye pedi-

cles). The anterior part of the fixed gena between the palpebral lobe and the marginal bend of the facial suture is roughly parallel-sided (Pl. 16, fig. 5b), or widening toward the eye socle (Pl. 20, fig. 1) or near the anterior margin of the shield (Pl. 8, figs. 2a, 2d). The carapace of the eye consists of a palpebral lobe, optic surface, socle\* and a pedicle. The palpebral lobes are highly elevated above the genal surface and risen above the glabella; only in some forms, they are leveled with the posterior part of the frontal lobe or even situated somewhat lower (Pl. 19, figs. 1b, 5b). The optical surface is fully developed and consists of hundreds of facets. There are zones of different curvature on this surface, i.e., lower cylindrical and upper spherical zones. The eye facets are arranged into parallel rows, these rows are oriented vertically in the cylindrical zone\* and in an oblique spiral in the spherical zone\*. The ratio of the zone widths is different in different species. The eye socle\* (part of the carapace between the optical surface and the pedicle or the genal surface) is rounded from below or hemispherical if the socle is fully developed (Pl. 13, fig. 1d), and cylindrical if the socle is not completely developed (Pl. 9, fig. 5b). The eye pedicles are present in several species of the genus *Asaphus* and in one of these species, may be very long (Pl. 13, fig. 1b), they probably are the longest amongst all known trilobites. The transverse section of the eye pedicle is elliptic. A developed eye pedicle is usually thinner than the eye socle (Pl. 13, fig. 1c, 2c) and only in *A. punctatus*, it is thicker than the eye socle (Pl. 11, fig. 5a). The eyes are usually approximated to the posterior margin of the cephalon (Pl. 6, fig. 2a), but may take the median position (Pl. 1, fig. 3a) or be somewhat closer to the anterior rather than to the posterior margin (Pl. 20, fig. 7b). The librigenae are convex (Pl. 6, fig. 4e), flat (Pl. 9, fig. 1b), or concave in their posterior parts (Pl. 10, fig. 4b). The inner margin of the genal doublure is sometimes expressed on the outer surface as a paradoublure furrow, which connects the depression of the fossula with the lateral termination of the posterior marginal furrow (Pl. 16, fig. 5b). The librigenae are sometimes provided with bordering\*, which does not occupy the entire anterolateral margin, but extends to the vincular pits only (Pl. 20, fig. 5). The genal corners are rounded (Pl. 19, fig. 1b), obtuse (Pl. 15, fig. 1c), or acuminate (Pl. 15, fig. 2a). In the last ontogenetic stages, and only these stages are known for the vast majority of forms in the subfamily, only some representatives of the genus *Subasaphus* possess the genal spines (Pl. 18, fig. 5). Articulation pits, which may be rather deep, are situated near the genal margins, at the line connecting the lateral margin of the shield and the doublure (Pl. 2, fig. 3c). These pits are invisible on the dorsal side (Pl. 8, fig. 2d) or expressed as a bend of the lateral margin of the shield (Pl. 5, fig. 4c) or as a deep incision (Pl. 19, figs. 1b, 2). In the genus *Onchometopus*, the vincular apparatus of the cephalon is represented by a long groove that extends along the entire anterolateral margin. The vincular apparatus is a device for tighter closing of the car-

apace, when a trilobite rolls up (Balashova, 1955; *Osnovy...*, 1960). The pleural terminations of the body segments are inserted into the pits or terminal parts of the groove, and the lateral margin of the pygidium occupies the rest of the groove of *Onchometopus* (Pl. 19, fig. 6b). Rings of the body rachis are flat (Pl. 19, figs. 8a, 8c) or convex (Pl. 19, fig. 4a). The acuteness of the pleural endings increases rearwards (Pl. 21, fig. 12). They may be rounded, acuminate, or even attenuated into short spines (Pl. 17, fig. 7d). The pygidium is rounded (Pl. 8, fig. 2e) or possesses straightened lateral margins and an acuminate (Pl. 16, fig. 6) or obtuse (Pl. 18, fig. 1e) posterior end. The pygidial rachis is smooth (Pl. 16, fig. 2d) or has traces of segmentation in the form of paired ridges, which are sometimes rather sharp, interrupted (Pl. 1, fig. 5) or not interrupted (Pl. 20, fig. 4a) on the rachial axis. These ridges appear to be rudimentary segments. The number of the segments reaches 7–8 or more. Posteriorly, the rachis is abruptly (Pl. 17, fig. 3) or weakly bordered (Pl. 16, fig. 7), or diffused (Pl. 19, fig. 7). The pleurae are smooth (Pl. 18, fig. 2e) or have traces of segmentation (Pl. 17, fig. 7c). The pleurae may have a concave bordering that may be noticeable behind of the rachis only (Pl. 13, fig. 4) or occupy the entire posterolateral margin of the shield (Pl. 20, fig. 4a). In species with deep vincular pits, thickenings, or vincular tubercles, are present at the lower margins of the facets\*.

The hypostome is large, occupies the whole length of the cephalon and nearly reaches its posterior margin (Pl. 21, figs. 1–3). Its posterior border bears a pair of wedge-shaped processes, which are triangular in plan and trapezoid in transverse section (wedge-shaped processes of the hypostome bordering\*). The anterior flanges are long and wide. The posterior flanges are small and triangular. The maculae are usually well-developed. According to Balashova (1953), such features of the hypostome as the angle of divergence of the wedge-shaped processes (erroneously named by her posterior flanges), the depth of the incision between them, and the expression of the maculae are species-specific.

The attachment of the hypostome to the carapace is firm; it is attached by the anterior margin and by the anterior margins of the anterior flanges to the doublure of the librigenae and by the upper flanges of the anterior flanges to the inner surface of the dorsal carapace beneath the fossulae (Pl. 21, figs. 2, 3; Fig. 20c) (Ivantsov, 1990b).

The carapace doublure is medium-wide, its inner margin runs in the middle of the librigenae on the cephalon, near the inner margin of the facets on the body pleurae, and in the middle of the pleurae on the pygidium, touching the rachis near its posterior end only (Pl. 3, fig. 1c).

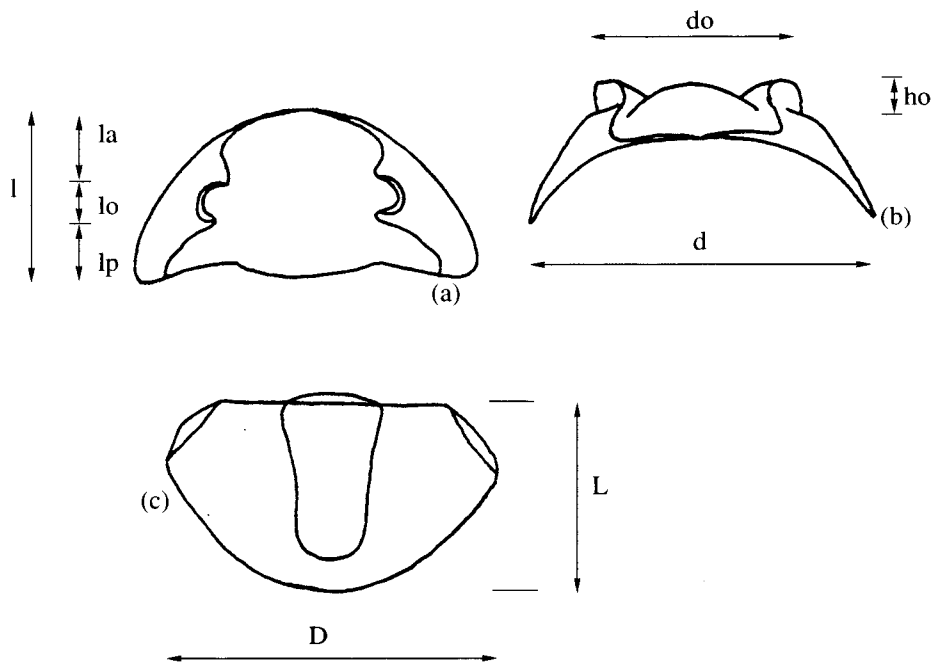
The panderian organs are represented by four types, i.e. asaphine\* (incisions on the genae and on the pleurae, genus *Onchometopus* and some species of the genus *Asaphus*), hemiasaphine\* (incisions on the genae

and on some pleurae and closed openings on the rest of the pleurae, *A. striatus*), neoasaphine\* (incisions on the genae and openings on the pleurae, *Xenasaphus*, *Delphasaphus*, and some species of the genus *Asaphus*), and subasaphine (openings on the genae and on the pleurae, genus *Subasaphus*). The panderian organs are absent from the pygidium. The anterior margin of a panderian organ is provided with a small protrusion. This protrusion is a part of the vincular apparatus. When the carapace rolls up, the pleura stops at its anterior side at the protrusion of the panderian organ of the preceding pleura or gena (Pl. 21, fig. 13) (Balashova, 1955, 1960).

The sculpture is represented by pits and terracelike folds. There are three types of pits, small, round, and evenly covering the outer surface of the carapace and the doublure with the hypostome ("pore openings" after Balashova, 1955), large, round, and rarely dispersed over the librigenae in some species ("openings of sensorial bristle canals," Balashova, 1955) (Pl. 10, fig. 7; Pl. 13, fig. 6), and large, angular, and situated on the eye socle. *A. knyrkoi* has an original pitted pattern of the sculpture, which consists of rounded pits intermediate between the first and the second type being evenly and densely scattered over the whole surface of the carapace (Pl. 12, fig. 6).

There are also three types of terracelike folds, short and twisted, usually low, arranged mainly on the dorsal side of the carapace (Pl. 1, fig. 1a; Pl. 16, fig. 8), straightened, long and high, widely separated, situated on the doublure and the hypostomal flanges and bordering (Pl. 3, fig. 1; Pl. 21, figs. 1, 2, 3), and straightened, short, frequent, very regular, developed on the inner, face-to-face situated sides of the wedge-shaped processes of the hypostomal bordering\* (Pl. 21, figs. 4, 5; Fig. 20c) (Ivantsov, 1990b). The presence of terracelike folds on some parts of the outer surface of the carapace is a diagnostic feature. These diagnostic folds, or D-folds, are situated on the frontal, medial, and basal lobes of the glabella (Pl. 1, fig. 1a), on the posterolateral margin of the ocular area, marginal parts of the librigenae, and on the anterior parts of the fixed genae (Pl. 16, fig. 8), on the occipital ring and rings of the body rachis (Pl. 7, fig. 3a), and on the pygidial rachis, where they may be arranged in the dorsal furrows or on the crests of the segments, emphasizing segmentation, on the longitudinal axis, being unconnected with segmentation (intercalary\* folds), on the pygidial pleurae, where they may be long and run radially from the rachis or short and nearly perpendicular to the longitudinal axis of the carapace (Pl. 1, fig. 6). A peculiar alternation of higher and lower terracelike folds ("thick and thin terracelike lines" in Balashova's descriptions (1953, 1976)) is observed on the pygidial doublure. These are most characteristic of *A. knyrkoi* (Pl. 12, fig. 5).

Measurements are shown in Fig. 21. Estimations like "large," "medium," "small" or "long," "medium," and "short," etc. have been made after analysis of the



**Fig. 21.** Measurements: (a, b) cephalon: (l) length, (d) width, (lo) eye socle length, (la) distance between eye and anterior margin of cephalon, (lp) distance between eye and posterior margin of cephalon, (ho) eye height, (do) distance between eye bases, (c) pygidium: (L) length, (D) width.

distribution of corresponding values in all measured specimens in the working collection.

The mean size of the carapace based on the cephalon width (d) in mm: small, less than 30; medium, ranging from 30 to 40 inclusive; large, greater than 45.

Proportions of the cephalon (ratio of its length to its width,  $l/d$ ): shortened (wide), less than 0.46; medium-proportionate, ranging from 0.46 to 0.52 inclusive; elongated, greater than 0.52.

Relative length of the eye (ratio of the eye length to the cephalon length,  $lo/l$ ): short, less than 0.25; medium, ranging from 0.25 to 0.33 inclusive; long, greater than 0.33.

Relative height of the eye (ratio of the eye height to its length,  $ho/lo$ ): low, less than 0.68; medium, ranging from 0.68 to 0.82 inclusive; high, greater than 0.82.

The position of the eyes with regard to the anterior and posterior margins of the cephalon (ratio of distances between the eye and the anterior margin and between the eye and the posterior margin,  $la/lp$ ): approximated to the anterior margin, less than 0.88; medium, ranging from 0.8 to 1.2 inclusive; approximated to the posterior margin, greater than 1.2.

The degree of separation of the eyes (ratio of the distance between the eyes to the cephalon width,  $do/d$ ): approximated, less than 0.52; moderately separated, ranging from 0.52 to 0.57 inclusive; widely separated, greater than 0.57.

The shape of the pygidium (ratio of the pygidium length to its width,  $L/D$ ): shortened (wide), less than

0.61; medium-proportionate, ranging from 0.61 to 0.75 inclusive; and elongated, greater than 0.75.

## 2.2. Some Data on the Ecology of the Asaphinae: Living and Taphonomical Environments

The correlation between the distribution of the Asaphinae trilobites and the depth of the paleobasin and the type of bottom sediment can be established for the Volkhov–Kunda time; the deposits of this time are most widespread in Baltoscandia. Asaphine fossils occur mainly in the gray organoclastic carbonate rocks of the northern Estonia–Lithuania confacial belt (Fig. 1a). In the deeper-water regions of Baltoscandia, where red limestones accumulated (Männil, 1966), they are rare. Asaphinae penetrated into the area of sedimentation of black clayey carbonate mud only sporadically, in the *lepidurus* and *expansus* time, when a general shallowing of the paleobasin occurred (Nielsen, 1992, 1995; Dronov *et al.*, 1998). On the Baltic–Ladoga Glinet, which is situated within the above-mentioned confacial belt, the depths are known to decrease westwards, i.e., from the shallow-water shelf to the littoral (Lamanskii, 1905; Orviku, 1960a, 1960b; Dronov, 2000); and in the same direction, the number of asaphine species declines up to their nearly complete disappearance from the sections. Therefore, asaphines inhabited the near-shore part of the basin but not the shallowest zone.

There are no data to reconstruct the environment of asaphines in more detail. Their fossils are unevenly dis-

tributed in the sections. Certain species occur within their stratigraphic range at a limited number of levels, and some of them only once, as *D. delphinus* known from a single approximately 10-cm-thick layer (Ivantsov, 1993b) (Figs. 10, 15). In neighboring sections these levels are apparently synchronous, as opposed to the levels from more remote sections. For example, the eastern part of the Baltic Glint (Ruditsa River) contains more evolutionary advanced forms of *A. ingrianus* (Pl. 8, fig. 4) and *A. punctatus* (Pl. 11, fig. 5), not known from the sections of the Ladoga Glint. Such a patchy stratigraphic distribution of these trilobites may be explained by the migration of the environments favorable for their burial.

Some characteristics of the common asaphine localities indicate that the hydrodynamic activity was higher in these environments and that the sedimentation was accompanied by sudden and catastrophic events. These are the sorting of remains (aggregations of similar-sized fossils are common, small specimens are rare, and larvae have not been never found); the absence of carapaces buried in the molting position; the absence of reliable traces of trilobites moving over the surface of and burrowing into bottom sediments; the predominance of fully articulated carapaces; and the presence of a large number of enrolled specimens (were some trilobites buried alive?). All these facts agree with Dronov's hypothesis (1998) that the sedimentation in the near-glint zone was of a storm-affected type. These asaphines most probably did not live where they were buried, but their movement (if any) cannot be long, because the carapaces were not disarticulated. The prevalence of molting casts (disarticulated during the molt) of juvenile specimens could be indicative of immediate proximity of the burial place to trilobite living grounds. Such asaphine localities are rare. On the Ladoga Glint they are confined mainly to the clayey limestones of the upper Lynna (Volkhov and Syas rivers) and middle Sillaoru (Lava River, Putilovo village) formations. What sort of local depositional conditions existed there during the accumulation of these sediments remains unknown.

An excellent example of nearly instant burial is the trilobite locality in the Valim Formation on the Volkhov River. Several huge aggregations of large carapaces of *X. devexus* have been discovered there (Fig. 17). In each aggregation all specimens are very similar in size and lie, being arranged in several layers, with their convex side directed downward. Their carapaces are disarticulated in the same manner: the head is detached, whereas the thorax and pygidium remain connected; the librigenae and hypostome are usually separated from the cranium. These aggregations contain two types of carapaces, more flattened and more convex ones. These facts suggest that (1) the very large carapaces approaching the maximal size of this species belong to mature individuals (the difference in the degree of convexity can be attributed to manifestations of sexual dimorphism); (2) most carapaces are repre-

sented by molting casts (the ontogenetically last, mass molt in arthropods usually precedes the collective coupling); (3) the identical and specific orientation of the carapaces and their arrangement into multilayered aggregations indicate that they were redistributed on the bottom due to hydrodynamic impact. It could be hypothesized that the locality has formed as a result of coincidence of the reproductive season and a great storm.

#### *Lifetime Damages*

The finds of carapaces with injuries that could be identified as lifetime damages are very rare. The collection under study contains only five such specimens.

(1) *A. expansus robustus* with an incision on the posterior margin of the pygidium from Balashova's collection (Pl. 21, fig. 9). The incision is situated in the left pleural area and is adjacent to the rhachis and triangular in shape. Its margins on the dorsal surface and on the doublure are drawn together, and the posterior end of the rhachis is slightly turned toward its side. It indicates that the wound has healed up.

(2) *S. laticaudatus* with incisions the right side of the pygidium and the two last thoracic pleura (Pl. 21, fig. 10). The defect of the pygidium consists of two incisions (parabolic and triangular in shape); the pleura are cut along the entire length of the facet. The edges of the damages have healed up.

(3) *A. kowalewskii* with the eyestalk broken and the edges of the wound healed was collected by M. Anosov and V. Zakharov (Pl. 21, fig. 7). The left eyestalk of this specimen is broken almost at its base, with the cuticle being drawn toward the eyestalk axis. The right eyestalk is also missing, but it was broken when the specimen was extracted from the rock.

(4) *A. laevissimus* with a perforation on the right gena (Pl. 21, fig. 6). The puncture situated on the right librigena near the facial suture has a rounded quadrangular shape elongated along the body axis, its edges are smooth. Inside the perforation an intact doublure margin is visible. When the specimen was acquired for the institute collection, the puncture was filled with rock, thus confirming that it had formed before lithification of the sediment. If this wound was inflicted during the animal's lifetime, it hardly could cause death, because no important internal organ were damaged; however, the animal probably died shortly thereafter, because the perforation bears no signs of healing or modification of surrounding tissues.

(5) *A. kowalewskii* with a perforation on the cephalon, collected by M. Legeev (Pl. 21, fig. 8). The puncture is situated on the right margin of the glabellar frontal lobe and is drop-shaped. The cuticle forms a shaft-like elevation around the puncture and continues deep inside it. The fact that the area of the cuticle that covers the inner slopes of the puncture is greater than the area of the puncture indicates that the cuticle formed inside

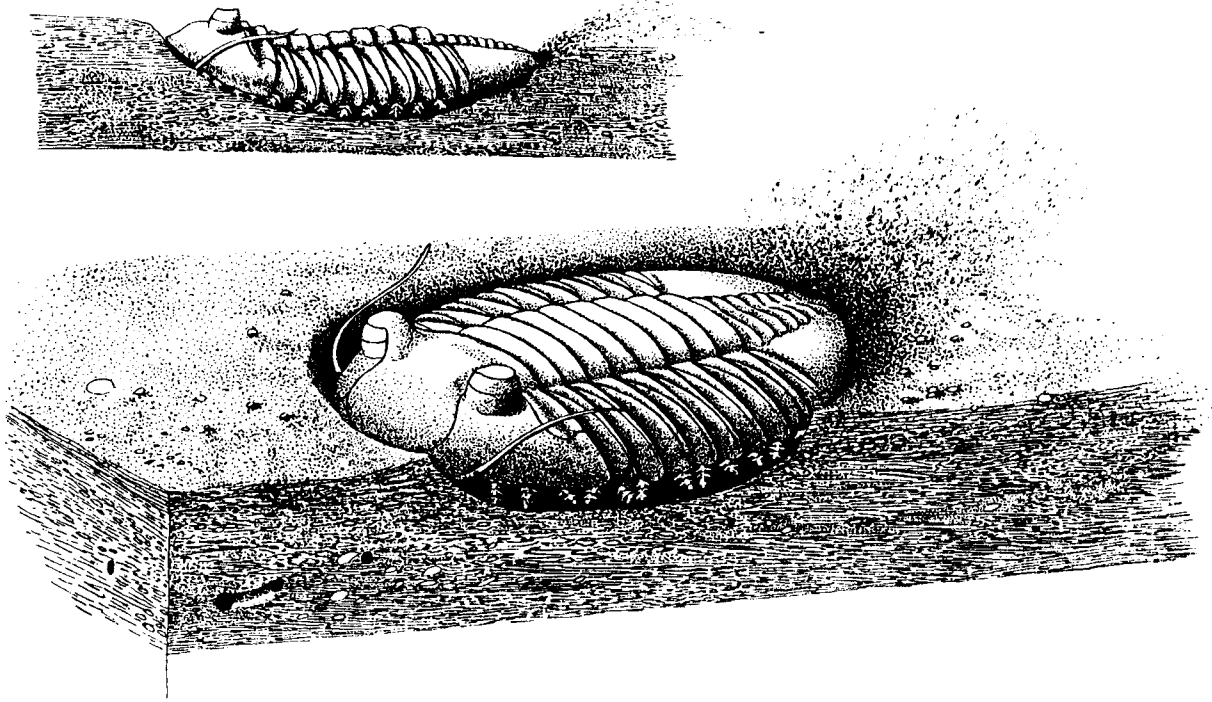


Fig. 22. Reconstruction of asaphid trilobite in normal position (its body is submerged into bottom sediment up to the eye bases, the anterior margin of the cephalon rises somewhat).

the puncture. Hence, the organism lived long after the trauma and an epithelial tissue capable of forming the cuticle was present inside the wound.

At present one cannot identify reliably the causes of the above-mentioned damages. The defects of the cutting character on the pygidia of *A. expansus* and *S. laticaudatus* could be produced by predators, e.g., cephalopods, whose beaks fit well the triangular contours of the incisions. Endoceratoid cephalopods constituted a usual component of the Baltic Ordovician biocoenoses and sometimes reached a huge size. For example, their 5-m-long shells have been found in the Aseri deposits on the Narva River (Ivantsov, 1992b). The wounds on the cephalons of *A. kowalewskii* and *A. laevissimus* could be mechanical, associated with the presumably burrowing mode of life of the Asaphinae.

#### *Supposed Mode of Life of the Asaphinae*

The morphological features of the carapace in the Asaphinae indicative, in our opinion, of the mode of life in trilobites of this subfamily are as follows: (1) thick-walled convex carapace; (2) deep furrows; (3) genal spines usually absent; (4) fully formed, highly elevated eyes; (5) numerous, coarse terracelike ridges present on the doublure (in all forms) and on the dorsal surface (in some forms); and (6) hypostome of a special type.

Trilobites of the genus *Asaphus* and some asaphid genera related to it possess the hypostome of a very distinctive shape (Pl. 21, figs. 1, 3). Its posterior margin bears two large winglike outgrowths of the flange, which are trapezoidal in cross section. Their inner sides facing each other are covered with very regular, asymmetric ribs (Pl. 21, figs. 4, 5), and the cuticle is thickest there. I suggested (Ivantsov, 1990b) that the hypostome of such a shape could be a part of the food-grinding apparatus, in which the ribbed faces were the immovable abrading elements. The increased mechanical load on the hypostome was compensated for by strengthening of its attachment to the cephalon: the asaphine hypostome is connected to the cephalon not only by its anterior margin and anterior sides of the first wing pair, as in other trilobites, but also by the upper sides of the anterior wings (Pl. 21, fig. 3; Fig. 21c).

The thick-walled convex carapace suggests that the animal was subjected to significant physical loads, and the well-developed furrows are indicative of relatively strong locomotory musculature (Osnovy..., 1960). Normally developed eyes, which are elevated very high in some forms, imply that during most of the time the organs of sight in these trilobites remained exposed to light, whereas their bodies could be situated beyond the sphere of normal vision, e.g., sunken into bottom sediments. The coarse terracelike ridges apparently evolved within the areas subjected to additional friction (Ivantsov, 1990b).

Taken together, these features suggest the burrowing mode of life in which the trilobite eyes were above the surface of bottom sediments and the distance from the ocular surface to the cephalon was equal to the burrowing depth (maximal in *A. kowalewskii*). Long genal spines, common in other asaphid trilobites posed an obstacle to this mode of life and, therefore, were usually absent. These trilobites most probably could not make burrows, because some forms possessed long, inflexible eyestalks incompatible with this life habit. They apparently dug narrow trenches in the upper layer of bottom sediments and usually remained there. Such prevailing location, along with a special shape of the hypostome adapted for grinding large food particles, suggests that the Asaphinae were predators feeding on the animal organisms found in the upper layer of bottom sediments (Fig. 22).

2.3. Evolution of the Subfamily Asaphinae in the Volkhov-Uhakian Time

The only evolutionary scheme for Baltic asaphines (= *Asaphus* sensu lato) was compiled by Balashova (1953). The morphological and stratigraphical data on which this scheme was based are now revised and shown to be incorrect in some respects. Balashova used a large body of data of earlier researchers without necessary criticism and apparently misidentified several species. For example, she mistook *A. eichwaldi* for *A. knyrkoi* (Balashova, 1953, pl. 5, figs. 6, 7) and united *A. striatus sarsi* with *A. raniceps* under the name *A. major* (Balashova, 1953 pl. 2, fig. 5); a great misinterpretation took place about trilobites of the groups *A. cornutus*, *A. latus*, *A. laevissimus*, and *Subasaphus*. Stratigraphic ranges of all (without exception) middle Kunda–Aseri species cited by Balashova (1953, 1976) are far from reality (Ivantsov, 1993b). Hence, the need for a new scheme. The graphical representation of the new scheme is given in Fig. 23. The textual description is given below; conclusions concerning phyletic rela-

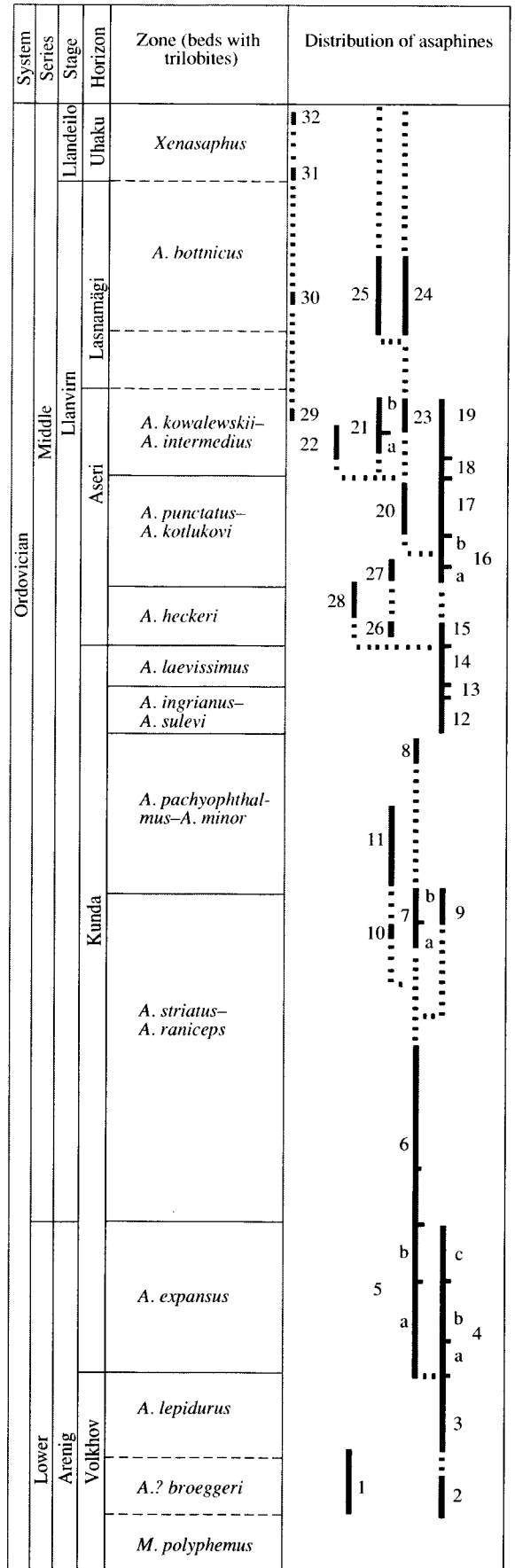


Fig. 23. Distribution of trilobites of the subfamily Asaphinae in the Ladoga Glint deposits and hypothetical scheme of phylogenetic relationships between their Ladoga representatives: (1) *Onchometopus volborthi*, (2) *Asaphus? broeggeri*, (3) *A. lepidurus*, (4) *A. expansus* ((a) *A. expansus gracilis*, (b) *A. expansus robustus*, (c) *A. expansus deltifrons*), (5) *A. acuminatus* ((a) *A. acuminatus lamanskii*, (b) *A. acuminatus acuminatus*), (6) *A. raniceps*, (7) *A. striatus* ((a) *A. striatus sarsi*, (b) *A. striatus striatus*), (8) *A. pachyophthalmus*, (9) *A. knyrkoi*, (10) *A. minutus*, (11) *A. minor*, (12) *A. sulevi*, (13) *A. ingrianus*, (14) *A. laevissimus*, (15) *A. heckeri*, (16) *A. kotlukovi* ((a) *A. kotlukovi kotlukovi*, (b) *A. kotlukovi tumidus*), (17) *A. punctatus*, (18) *A. intermedius*, (19) *A. kowalewskii*, (20) *A. cornutus*, (21) *A. plautini* ((a) *A. plautini polyxenus*, (b) *A. plautini plautini*), (22) *A. latus*, (23) *A. holmi*, (24) *A. bottnicus*, (25) *Asaphus? ornatus*, (26) *Subasaphus latisegmentatus*, (27) *S. spinifer*, (28) *S. laticaudatus*, (29) *Delphasaphus delphinus*, (30) *Xenasaphus* sp., (31) *X. mjannili*, (32) *X. devexus*.

tionships have been drawn on the basis of closeness of morphology and stratigraphic ranges.

(1) *A. ? broeggeri* is the earliest member of the genus *Asaphus*; some features of its morphology (see Systematic Paleontology) cast doubt on its assignment to the genus; however, at present there are no sufficient data to place it elsewhere. The origin of this species (and, therefore, of the genus) remains uncertain.

(2) *A. lepidurus* is separated from the above species by some stratigraphic interval and significantly differs from it in having clearly developed basal lobes, high eyes, posterior margin of the ocular area not ridged, etc. However, already the late *A. ? broeggeri* show a tendency toward the formation of basal lobes (especially noticeable on internal molds), more convex dorsal surface, and deeper cephalic furrows. Therefore, the origin of *A. lepidurus* from *A. ? broeggeri* is quite probable. *A. lepidurus* is the first true *Asaphus*.

(3) *A. expansus* immediately follows *A. lepidurus* in the sections. The early representatives of the subspecies *A. expansus gracilis* differ from the late *A. lepidurus* in fact only in the shorter cephalon; thus, the species doubtless descended from *A. lepidurus*.

(4) *A. acuminatus* is rare, and only a few specimens have been stratigraphically allocated; most of them originate from the upper part of the species' stratigraphic range. The only specimen of *A. acuminatus lamanskii* from the base of the *expansus* Zone is similar to *A. lepidurus* in many respects; however, it already possesses a characteristic feature of the subspecies, very small eyes, as well as lens-shaped basal lobes. The species most probably descended from *A. lepidurus*, but one cannot exclude the possibility that it descended from *A. ? broeggeri* (it resembles the latter in having poorly developed basal lobes, all furrows shallow, and the pygidial rhachis weakly segmented), although the stratigraphic interval separating them is quite considerable.

(5) *A. raniceps*. There is a nearly uninterrupted morphological series, *A. acuminatus lamanskii*–*A. acuminatus acuminatus*–*A. raniceps*, in which the taxa differ in fact only in the eye size and degree of the pygidial rhachis segmentation. Stratigraphically, these taxa immediately follow one another in the sections and apparently constitute a single phyletic lineage.

(6) *A. striatus* is separated from *A. raniceps* by a considerable stratigraphic interval, containing representatives of the genus so poorly preserved that their remains cannot be studied or even prepared more or less satisfactorily. Despite the time interval separating them, members of the subspecies *A. striatus sarsi* are so similar to the late *A. raniceps* that sometimes they were united into one species, *A. major* (Lamanskii, 1905; Balashova, 1953). *A. striatus* quite probably descended from *A. raniceps*.

(7) *A. pachyophthalmus* is separated from *A. striatus* by a long stratigraphic interval and differs from it markedly. However, they bear some similarities, and the species may be considered as the terminal member in the

phyletic lineage *A. acuminatus*–*A. raniceps*–*A. striatus* in terms of the degree of the development of eyes and vincular pits. *A. pachyophthalmus* apparently descended from *A. striatus striatus*. The intermediate forms, which probably existed between them, remain unknown.

(8) *A. minor* is in many respects similar to its stratigraphic precursor, *A. striatus striatus*, and also quite similar to *A. minutus*, which existed even earlier. The origin of the species is uncertain. Moreover, the entire group of middle Kunda forms (*A. striatus striatus*, *A. striatus sarsi*, *A. pachyophthalmus*, *A. minutus*, *A. minor*, *A. knyrkoi*, and fossils of uncertain affinities) needs detailed study, which should start with collecting additional material, which is very difficult for this part of the section.

(9) *A. knyrkoi* is very distinct from the others in several characters, especially in the details of the cuticular ornamentation. Its origin is uncertain; possibly it descended through a series of intermediate forms from *A. expansus*, resembling the latter in the shape of the cephalon and incipient (in *A. expansus deltifrons*) fine terracelike ridges on the anterior glabellar slope. The similarity between these species was noted already by Lamanskii (1905), who supposed the origin of *A. eichwaldi* var. *expansoides* Lamanskii (= *A. knyrkoi*) from *A. expansus*. However, there are more differences than similarities, and the stratigraphic hiatus between the species is great.

(10) *A. sulevi* is quite variable: some forms resemble *A. knyrkoi*, and both species were sometimes united (Schmidt, 1901; Lamanskii, 1901, 1905; Balashova, 1953); other forms are similar to *A. pachyophthalmus*. However, there are essential differences from both species (those from *A. knyrkoi* are more significant). Therefore, the origin of the species and the entire late Kunda–Azeri group of species remains uncertain.

(11) The species chain *A. sulevi*–*A. ingrianus*–*A. laevissimus*–*A. heckeri* represents a nearly continuous series of morphological changes with gradual accumulation of the features characteristic of the Aseri *Asaphus*: a sharp bend of the anterior branch of the facial suture appears in *A. ingrianus*; eye lists, in *A. laevissimus*; the tubercles at the posterolateral corners of ocular areas, in *A. heckeri*.

(12) *A. kotlukovi* is similar to *A. heckeri*, occurs higher in the section, and, most probably, descended from the latter.

(13) The chain of forms replacing each other in the section *A. kotlukovi kotlukovi*–*A. kotlukovi tumidus*–*A. punctatus*–*A. intermedius*–*A. kowalewskii* again demonstrates a nearly continuous series of morphological changes. All these species are doubtless related.

(14) *A. cornutus* descended from *A. kotlukovi tumidus* through the form with weak terracelike ridges on the lateral slopes of the ocular areas.

(15) *A. holmi* resembles *A. cornutus* but possesses higher eyes, coarser terracelike ridges on the cephalon, and a somewhat different shape of the pygidium.

It occurs higher than *A. cornutus* in the section and obviously has descended from this species.

(16) *A. plautini* and *A. latus* show the greatest morphological similarity to their precursor, *A. cornutus*, and apparently descended from the latter.

(17) *A. bottnicus* is separated from its precursors by a significant interval of the section and differs from them considerably. Of the latest Aseri forms it stands closest to and possibly descended from *A. holmi*. *A. bottnicus* completed the Arenig–Llanvirn phase of the evolution of the genus *Asaphus*, when representatives of this genus along with the members of the genus *Iliaenus* dominated the communities. In the younger deposits asaphine fossils occur sporadically, in few specimens, and remain almost not studied.

(18) Until recently, *A. ? ornatus* was united with *A. bottnicus* into a single species (*A. ornatus*). These species are indeed similar and most probably have a common origin. *A. ? ornatus*, displaying many morphological characters of the genus *Ogmasaphus*, stands near the point of divergence of these genera and is possibly ancestral to *Ogmasaphus*.

(19) *S. latisegmentatus* bears a great similarity to *A. heckeri* cooccurring with it in the section and even a greater similarity to the preceding *A. laevis* and *A. ingrianus*. One cannot exclude that it descended from one of these species. The species is the earliest member of the genus *Subasaphus*.

(20) *S. laticaudatus* is similar to its immediate precursors in the section, *A. heckeri* and *S. latisegmentatus*. The presence in the latter of specimens with rudimentary genal spines and a broad pygidium makes these species almost indistinguishable. The species probably descended from *S. latisegmentatus*.

(21) *O. volborthi*. The species and the genus are isolated in the system of the subfamily, with no related species both in the underlying and overlying strata.

(22) *D. delphinus*. The ancestral species is unknown; possibly, it was a member of the genus *Asaphus* or *Onchometopus*.

(23) *X. mjannili* and *X. devexus*, distinctly differ from *D. delphinus* in some features and resemble it in many others. They could be descendants of this latter through a series of intermediate forms not preserved in the section. The genus *Xenasaphus* already existed in the *bottnicus* phase, as evidenced by the find of an isolated pygidium undeterminable to the species in the middle Porogi Formation on the Volkhov River. The sequence of speciation in this genus is unclear: *X. devexus* occurs higher than *X. mjannili* in the section but is closer than the latter to *D. delphinus* in one of its morphological characters (low-placed eyes). The problem remains unsolved so far as, on the one hand, this character may prove to be adaptive and, thus, not indicative of the degree of relationship and, on the other hand, the data on the stratigraphic range of *X. mjannili* derived from a single section could be incomplete.

When studying the phylogeny of the genus *Asaphus* s. l., Balashova (1953) hypothesized about an explosive speciation at the Volkhov–Obukhovo boundary from a single species that existed in the *A. lepidurus*–*M. gibba* time to the four new species in the *A. expansus*–*A. lamanskii* time and another at the Obukhovo–Duboviki boundary, from a single species existing in the *A. major* time to the eight in the *A. eichwaldi*–*A. minor* time. She attributed these changes in speciation rate to the major reorganizations of the paleobasin that in her opinion took place at these boundaries (Balashova, 1953). Recent data on the stratigraphic ranges of asaphines contradict this assumption. As judged from materials from the Ladoga Glint, in the Volkhov–Lansnamägi time one or two, or more rarely, three trilobite species of this subfamily existed synchronously. The evolution rates were more or less constant (Fig. 23). The only event of explosive speciation occurred in the late Aseri time (when the beds with *A. kowalewskii* were deposited and five species of the subfamily coocurred). However, there are no data on any changes in the depositional conditions or other parameters of the paleobasin during this time interval.

#### 2.4. Systematic Paleontology of the Subfamily Asaphinae

The systematics of the subfamily Asaphinae, as well as the systematics of the whole superfamily Asaphoidea Burmeister, 1843 is currently in a state of flux. In this work, we follow the last published system of the subfamily Asaphinae by Balashova (1976). Although not good, it still remains the only carefully elaborated system of asaphines. The diagnosis of the subfamily Asaphinae, as well as generic and specific diagnoses, have been entirely revised by me. In contrast to Balashova's paper, I pay greater attention to the characters that are expressed on the outer surface of the carapace, which is easier to observe.

According to Balashova, the subfamily Asaphinae comprises the genera *Asaphus* Brongniart, *Onchometopus* Schmidt, and *Xenasaphus* Jaanusson. In the present work, the subgenera *Asaphus* (*Subasaphus*) Balashova, 1976 and *Xenasaphus* (*Delphasaphus*) Ivantsov, 2000 are raised to generic rank.

In *Asaphus*, Schmidt (1901) included two subgenera, *Asaphus* sensu stricto and *Onchometopus* (Table 3). In 1953, in an interval of several months, Jaanusson (1953a) and Balashova (1953) published revisions, where new subgeneric names *Schizophorus* Balashova (= *Asaphus* Brongniart) and *Trematophorus* Balashova (= *Neoasaphus* Jaanusson) appeared. Later Balashova (1976) established three more subgenera, *Multiasaphus*, *Subasaphus*, and *Postasaphus*. The main feature used for separation of the subgenera *Asaphus*, *Neoasaphus*, and *Subasaphus* was the structure of the panderian organs. However, the tendency to closure and partial fusion of the panderian organ fissures is independently expressed in many groups of the asaphine

**Table 3.** Composition of the genus *Asaphus* according to different authors

Schmidt, 1901	Jaanusson, 1953	Balashova, 1953	Balashova, 1976	Ivantsov, 1997
<i>Asaphus</i>	<i>Asaphus</i>	<i>Schizophorus</i>	<i>Asaphus</i>	<i>Asaphus</i>
	<i>Neosaphus</i>	<i>Trematophorus</i>	<i>Neosaphus</i>	<i>Neosaphus</i>
				<i>Kundasaphus</i>
				<i>Eichvaldiasaphus</i>
				<i>Cornasaphus</i>
			<i>Multiasaphus</i>	<i>Multiasaphus</i>
<i>Postasaphus</i>	<i>Postasaphus</i>			
<i>Subasaphus</i>	genus			
<i>Onchometopus</i>	<i>Onchometopus</i>	genus	genus	genus

trilobites. These changes appear to occur independently in different evolutionary lines within the genus *Asaphus* as well. In addition, different populations of the same species might possess different types of panderian organs. For example, they are asaphine in *A. striatus* specimens from Norway (Wandas, 1983) and hemiasaphine in specimens from the Leningrad Region; the case of the *A. laevis* panderian organs may be mentioned here, they are subasaphine according to Balashova (1976) and neosaphine according to my observation (Ivantsov, 1992a).

I attempted to rank some phyletic lines as subgenera of *Asaphus* (Ivantsov, 1997). However, these subgenera turned out to be impossible to define, since the most distinctive features appear, develop, and disappear within a line. Transition forms between two lines may be free of features of either of them, and the assignment of such forms to a subgenus is mostly arbitrary. That is why the subgeneric category is not used in the present work.

The majority of asaphine species demonstrates a high morphological variability, which is rather difficult to describe. In some species, forms can be recognized. If forms of one species are distinguished securely by their stratigraphic range, they are treated as subspecies.

In her earlier work on asaphids, Balashova (1953) simultaneously selected a lectotype in Schmidt's collection and a neotype in her collection even for species that were not described by Schmidt and for those whose type series were preserved and contained specimens clearly demonstrating specific characters. Possibly, some of the type collection was already missed at that time; however, it is difficult to understand why lost specimens were designated as lectotypes, while the type series were mainly preserved. Balashova did not explain this procedure. Afterwards, Balashova (1976) renamed all her lectotypes holotypes. That action contradicts Article 73 and is covered by Article 75.2 of the International Code of Zoological Nomenclature (ICZN, 2000), so the neotypes from Balashova's collection (1953) and the holotypes from Schmidt's collection (Balashova, 1976) are not valid. Neotypes may be kept

for three species only, i.e., *A. lepidurus* Nieszkowski, *A. kowalewskii* Lawrow, and *A. laevis* F. Schmidt, since their lectotypes have been designated incorrectly.

#### CLASS TRILOBITA WALCH, 1771

Order Ptychopariida Swinnerton, 1915

Superfamily Asaphoidea Burmeister, 1843

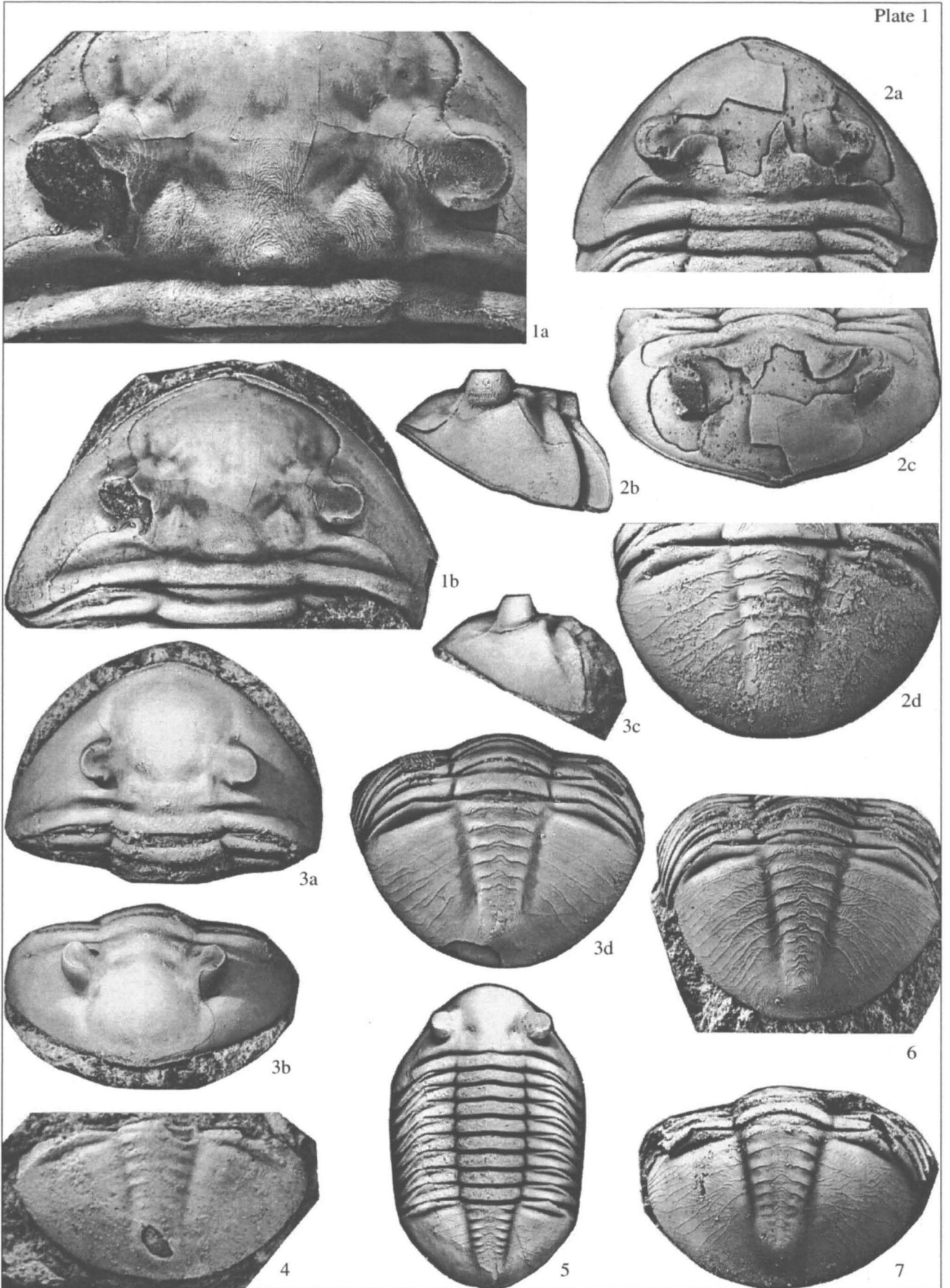
**Family Asaphidae Burmeister, 1843**

**Subfamily Asaphinae Burmeister, 1843**

**Description.** Trilobites of this subfamily possess a large carapace, reaching 10 mm (hereinafter measurements are obtained from East Baltic representatives of the group). The carapace is convex and thick-walled. The cephalon is rounded triangular; on average, its length is 0.5 times as long as it is wide, the mean l/d is between 0.46 and 0.52. The mean width of the cephalon is 30–45 mm. The anterior border of the cephalon is rarely straight (horizontal), usually curved in the beaklike manner, sometimes sharply curved. The glabella is wide, convex, shifted toward the anterior border, and slightly hangs over the latter in some species. The glabella is divided by the transverse flexure into a large pearlike (*Asaphus*, *Subasaphus*, and *Xenasaphus*) or rhomboid (*Delphasaphus*) frontal lobe and a small trapezoid medial lobe. In some species, a ridge or a shallow depression stretched along the glabellar axis develops in the anterior part of the frontal lobe. The medial lobe usually bears the medial tubercle. Two to three pairs of elongate tubercles, apparently representing rudiments of the frontal lobes of the glabella and which are the most visible in molds, occasionally (in some *Asaphus*) develop on the lateral margins of the frontal lobe. One pair of wide and rather deep furrows separates lenslike or trapezoid basal lobes from the medial lobe. The glabella is not subdivided into lobes in the genus *Onchometopus*. The depth of the preglabellar furrow varies; the furrow itself may be lacking. The dorsal furrows on the frontal lobe are more or less distinct, those on the basal lobes are shallow and usually

poorly defined. In the latter case, glabellar furrows form substituting pseudodorsal furrows (in some *Asaphus*). The fossulae are usually present and developed as more or less diffused depressions bordering the dorsal furrows frontally. The occipital furrow is either deep or shallow, or is shaped as an isolated pit, or is absent. The occipital ring is flat or convex. The anterior branch of the facial suture has three bends. The distance between the anterior facial sutures at the level of the marginal bends is much greater than the distance between them at the level of the eye socles (except for the species possessing a well-developed eyestalk). The anterior end of the cranidium is obtuse, acuminate, or lingulate. The anterior part of the fixed cheek is parallel-sided or widens anteriorly (in *Subasaphus*) or toward the palpebral lobes (in *Xenasaphus*). The librigenae are convex, flat, or concave in their posterior parts. The eyes are relatively large, except for a single case of *A. acuminatus lamanskii*. In *Asaphus*, the palpebral lobes are highly raised above the cheeks and elevated above the posterior part of the frontal lobe of the glabella; in *Onchometopus*, in some *Xenasaphus*, *A. expansus deltifrons*, and *Subasaphus platyurus*, they are leveled with the posterior part of the frontal lobe or situated below it. The visual surface of the eyes is fully developed, the eye socles may be underdeveloped, but usually they are developed completely. A fully developed eye socle has the form of a hemisphere, a weakly developed socle forms a low cylinder. The ocular pedicles are present in several species of the genus *Asaphus*, being very long in one of the species, *A. kowalewskii*. The transverse section of the ocular pedicles is elliptical; its long axis is either less or greater than the long axis of the section of the eye socle. The mean ratio of the eye socle length to the length of the cephalon is 0.25–0.33, the ratio of the eye height to the eye socle length is 0.68–0.82. The eyes are usually close to the posterior margin of the cephalon but may be median or rarely somewhat closer to the anterior margin than to the posterior margin (*Xenasaphus devexus* and one of *A. lepidurus* varieties). The distance between the eye bases (the ocular pedicles or eye socles, when the ocular pedicles are absent) is approximately half as long as the cephalon width (0.52–0.57). In *Xenasaphus* and in some species of *Asaphus*, a ridgelike inflation, possibly analogous to the eye list of other trilobites, stretches from the eye socle to the lobe rudiments on the frontal lobe of the glabella. In many species of the genus *Asaphus*, the ocular area is separated as a swelling. In some species of the genus *Asaphus*, there is a tubercular swelling in the posterior outer corner of the ocular area; there is a distinct crestlike ridge running along the posterior margin of this area in *A. ? broeggeri*. In *Xenasaphus* and *Delphasaphus*, the anterolateral margin of the cephalon bears a narrow border that stops near the anterior margin of the vincular pits and is absent from the genal corners. The inner margin of the genal doublure is sometimes expressed on the outer surface as a para-doublure furrow that connects the fossula with lateral

termination of the marginal furrow. The articulation pits, which are sometimes deep and sometimes nearly not expressed, are situated near the genal corners on the line connecting the lateral margin of the shield and the doublure. In *Onchometopus*, a groove stretches along the entire anterolateral margin of the shield instead of the pits. The pits are not visible from the dorsal side; otherwise they are expressed as a bend of the lateral margin of the shield (*Xenasaphus*) or a deep incision (*Delphasaphus*). The genal corners are rounded (*Delphasaphus*), obtuse, or acuminate (*Asaphus*). During the last ontogenetic stages (only these stages are known for the vast majority of asaphines), only a few representatives of the genus *Subasaphus* possess genal spines. Rings of the rachis are either flat (as in *Subasaphus*) or convex (as in *Onchometopus*). The pleural terminations are rounded (*Xenasaphus*), angular (most *Asaphus*), or acuminate and attenuated as short spines (*A. ? ornatus*). The pygidia have rounded or straightened lateral and posterior margins, i.e., they are semirounded (some *Asaphus*), rounded triangular (*Delphasaphus*), or rounded pentagonal (*S. laticaudatus*). The mean ratio of the length of the pygidium to its width is 0.55–0.61. The pygidial rachis is long and smooth or has traces of a subdivision in the form of paired ridges, which are probably rudimentary segments. The number of segments is seven or eight and more. The segments are usually disrupted at the rachis axis (*Asaphus* and *Onchometopus*), rarely not (*Xenasaphus* and *Delphasaphus*). The rachis is sharply delineated or diffused from behind. The pleurae are convex to flattened, smooth, or, more rarely, with segmentation traces expressed as ill-defined ridges that radially run from the rachis. Thickenings (vincular tubercles) are present on the lower margins of facets in species possessing deep vincular pits. A small bordering is developed behind the rachis in two species of the genus *Asaphus*; in the genus *Xenasaphus*, all representatives have a broad concave bordering along the entire posterior margin of the pygidium. The hypostome is large, occupies the whole length of the cephalon, reaching its posterior margin; its posterior border bears a pair of wedge-shaped processes, which are triangular from above and trapezoid in the transverse section. The anterior flanges are long, wide and flat, connected by one margin with the genal doublure and by the other side, touching the inner surface of the carapace below the fossulae. The posterior flanges are small and triangular. The carapace doublure is of medium width; on the cephalon, its inner margin runs through the middle of the librigenae; on the pygidium, it runs through the middle of the pleurae touching the rachis near its posterior end only; on the pleurae of the body, it runs along the inner margin of the facets. There are four types of panderian organs, asaphine (incisions on the genae and pleurae in the genus *Onchometopus* and in some species of the genus *Asaphus*), hemiasaphine (incisions on the genae and some pleurae and closed holes on the rest of the pleurae in *Asaphus striatus*), neosaphine (incisions on the genae



and holes on the pleurae in *Xenasaphus*, *Delphasaphus*, and some species of the genus *Asaphus*, and subasaphine (holes on the genae and pleurae in the genus *Subasaphus*). The panderian organs are absent from the pygidium. The ornamentation is represented by pits and terracelike folds.

**Composition.** Five genera, *Asaphus* Brongniart, 1822, *Onchometopus* F. Schmidt, 1898, *Xenasaphus* Jaanusson, 1953, *Subasaphus* Balashova, 1976, and *Delphasaphus* Ivantsov, 2000.

**Comparison.** Unlike other subfamilies of Asaphidae, representatives of this subfamily are characterized by a complete or nearly complete absence of the preglabellar field and the border of the cephalon, the obtuse or rounded posterior margin of the pygidium (it is mainly concave in Proasaphinae and acuminate in Lisogoritinae), the absence or concavity of the border of the pygidium.

**Occurrence.** Baltoscandia; Lower–Middle Ordovician, Arenig–Caradoc.

### Genus *Asaphus* Brongniart, 1822

*Asaphus*: Brongniart, 1822; Dalman, 1828, p. 41; Angelin, 1854, p. 51; Brögger, 1882, p. 86; Schmidt, 1898, p. 16; 1901, p. 4; Zittel, 1934, p. 951; Lesnikova and Weber, 1949, p. 278; Jaanusson, 1953a, p. 391; 1959, p. 335; Balashova, 1953, p. 386; 1960, p. 143; 1976, p. 6; Hupé, 1955, p. 200.

**Type species.** *Entomostracites expansus* Wahlberg, 1821.

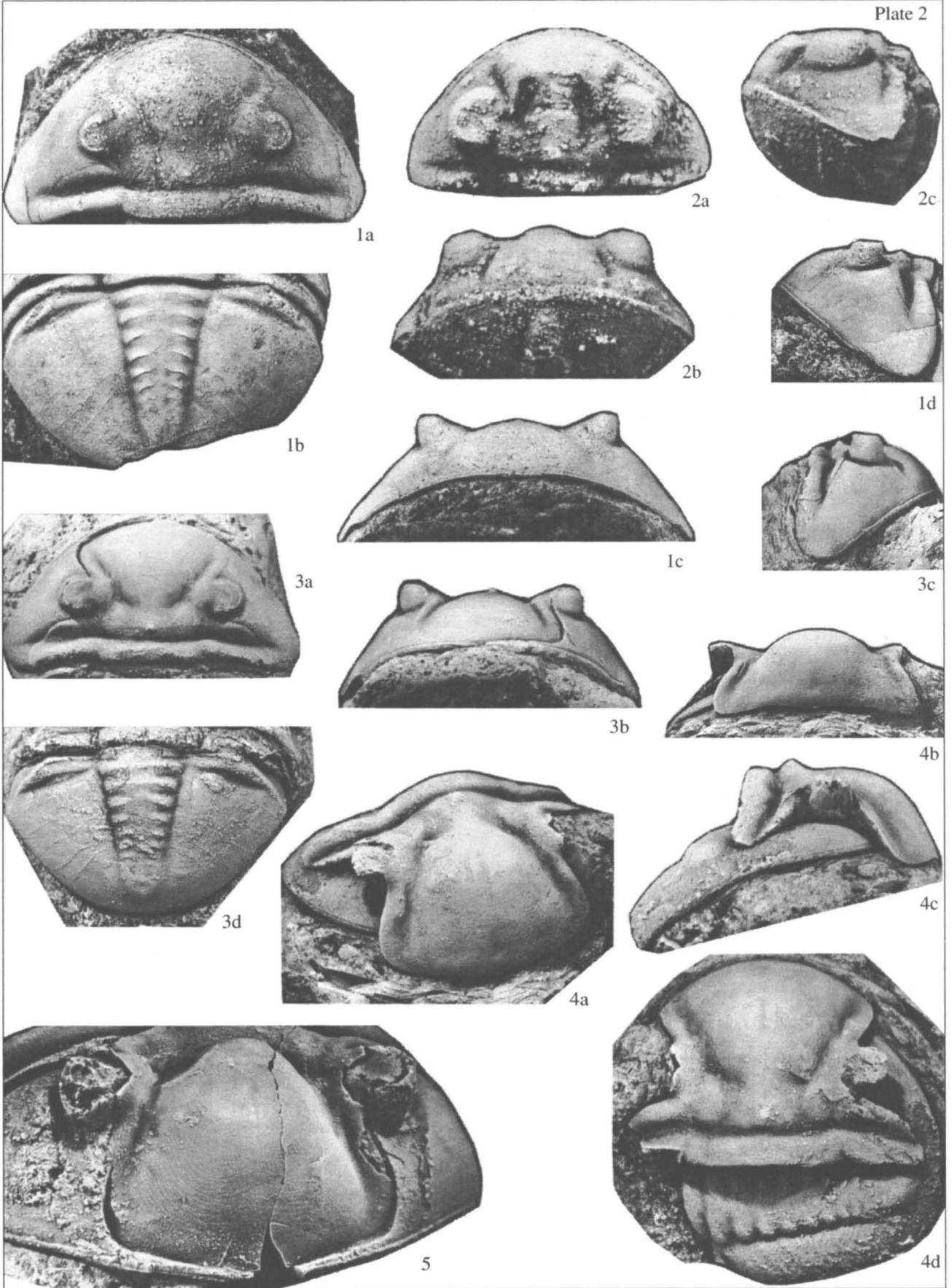
**Diagnosis.** Cephalon shortened to elongated; basal lobes present; eyes usually highly elevated, sometimes with pedicles; genal corners without corners; vincular apparatus represented by pits of various depth, sometimes absent; pygidium shortened to elongated; bordering on cephalon and pygidium absent or represented by small flexure behind rachis; panderian organs asaphine, hemiasaphine, or neoasaphine.

**Description.** The trilobite are usually large. The carapace may reach 110 mm, while the cephalon may reach 65 mm. The cephalon is short to elongated and is rounded or acuminate frontally. The anterior margin of the cephalon is horizontal, but usually is curved in the beaklike manner. The glabella is subdivided into large pearlike frontal and small trapezoid medial lobes, which sometimes are fused together but more often are separated by a shallow furrow or flexure.

The frontal lobe does not reach the anterior margin or reaches and overhangs it. The preglabellar groove is weak or absent. The medial lobe usually bears the medial tubercle. One pair of ill-expressed (in the relief) basal lobes are lenslike or trapezoidal. The lateral margins of the frontal lobes sometimes bear two or three pairs of rudimental lobes. Representatives of some species have an axially elongated keel-like ridge or shallow depression in the anterior part of the frontal lobe. The dorsal furrows of the frontal lobe are more or less clear, those of the basal lobes are shallow and often poorly visible; pseudodorsal furrows are formed in the latter case. The fossulae are usually present. The occipital furrow is either deep or shallow, or formed as an isolated pit, or absent. The occipital ring is flat or convex. A lingulate pointing is often present at the anterior end of the cranidium. The distance between the anterior branches of the facial fissures at the level of the marginal flexures is greater than such a distance at the level of the eye socles (except for the species with well-developed eye pedicles). The anterior part of the fixed gena is parallel-sided or widens near the anterior margin. The librigenae are convex, flat, or concave in their posterior part. The eyes are short to long, usually medium-high and high, more rarely, low. The palpebral lobes are strongly elevated over the genae and elevated over the posterior part of the frontal lobe, in *A. expansus deltifrons* only, they are situated at the same level with the posterior part of the frontal lobe or even somewhat lower than the latter. The eyes are usually shifted to the posterior margin of the cephalon, rarely take the median position, and in one variety of *A. lepidurus*, they are somewhat closer to the anterior part of the cephalon. The eye socles are usually fully developed, rounded from below; more rarely they are underdeveloped, cylindrical. The eye pedicles are widely developed in a number of species close to *A. cornutus*, they are notably long in two of these species. A developed eye pedicle is usually thinner than the eye socle and is thicker than the latter in *A. punctatus* only. The ocular ridge is developed in some species. In several species, the ocular area is separated as an elevation. A tubercle is occasionally situated in the posterior outer corner of the ocular area, in *A. ? broeggeri*, a quite distinct crestlike ridge runs along the posterior margin of this area. The marginal bordering is absent from the cephalon. The paradoublural furrow is sometimes present. Artic-

### Explanation of Plate 1

**Figs. 1–7.** *Asaphus lepidurus* Nieszkowskii, 1859; Volkhov Horizon, Volkhov Formation, Frizy and Khamontovo members, beds with *A. lepidurus*: (1) specimen PIN, no. 4330/69, cephalon: (1a) terraced folds of occipital region,  $\times 5.5$ , (1b) general appearance,  $\times 3$ , right bank of the Volkhov River near the village of Obukhovo, Frizy Member, collected by Balashova; (2) specimen PIN, no. 4330/11, unrolled carapace of peculiar shape, with large eyes approximated to anterior margin,  $\times 1.5$ ; (2a–2c) cephalon: (2a) dorsal view, (2b) side view, (2c) view from the frontal lobe, (2d) pygidium, Lynna River, Lynna Mouth outcrop, Frizy Member, 1.6 m above the floor; (3) specimen PIN, no. 4330/10, rolled carapace,  $\times 1.5$ ; (3a–3c) cephalon: (3a) dorsal view, (3b) view from the frontal lobe, (3c) side view, (3d) pygidium Putilovo outcrop Khamontovo Member, talus; (4) specimen PIN, no. 4330/145, shortened pygidium of one of the earlier representatives of the species,  $\times 2$ , Lynna River, Lynna Mouth outcrop, Frizy Member, 0.5 m above the floor; (5) specimen PIN, no. 4330/174, unrolled restored carapace,  $\times 1$ , Lava River, Gorodishchenskii Kar'er outcrop, about 1 m below the roof of the Volkhov Formation; (6) specimen PIN, no. 4330/68, pygidium,  $\times 1.5$ , Putilovo outcrop; (7) specimen PIN, no. 4330/66, pygidium of small specimen,  $\times 2.5$ , left bank of the Volkhov River, village of Izvoz, collected by Balashova.



ulation pits are rather deep, sometimes irregular, usually poorly visible from the outer face of the carapace. The genal corners are rounded, obtuse, or acuminate, devoid of spines in adults. The occipital ring and rings of the rachis are flat or convex. The pygidium is either rounded or parallel-sided and has a rounded, acuminate, or obtuse posterior margin; its length is usually slightly greater than its width. The pygidial rachis is long and smooth or has traces of subdivision, which are sometimes rather distinct, and is sharply or weakly bordered from behind. A narrow, weakly expressed concave bordering is developed behind the rachis in two species. The pleurae are flattened or convex, smooth or have traces of segmentation. The facets widen toward the lateral corners of the pygidium. The panderian organs are asaphine, hemiasaphine, and neasaphine. Terracelike folds maybe present in any part of the outer surface of the carapace.

**Species composition.** *A. expansus* (Wahlenberg, 1821), *A. lepidurus* Nieszkowski, 1859, *A. acuminatus* Boeck, 1838, *A. raniceps* Dalman, 1828, *A. striatus* Boeck, 1838, *A. minutus* sp. nov., *A. minor* F. Schmidt, 1901, *A. pachyophthalmus* F. Schmidt, 1901, *A. knyrkoi* F. Schmidt, 1901, *A. sulevi* Jaanusson, 1953, *A. ingrianus* Jaanusson, 1953, *A. laevisimus* F. Schmidt, 1901, *A. heckeri* Ivantsov, 2000, *A. kotlukovi* Balashova, 1953, *A. punctatus* Lesnikova, 1949, *A. intermedius* Balashova, 1953, *A. kowalewskii* Lawrow, 1856, *A. cornutus* Pander, 1830, *A. holmi* F. Schmidt, 1901, *A. plautini* F. Schmidt, 1901, *A. latus*, *A. bottnicus* Jaanusson, 1953, *A. ? broeggeri* F. Schmidt, 1901, *A. ? ornatus* Pompeckii, 1890, also several species from the Baltic Region and Sweden (Törnquist, 1884; Wiman, 1908; Schmidt, 1901; Balashova, 1953, 1976; Jaanusson, 1953a, 1953b).

**Comparison.** This genus differs from the genus *Subasaphus* in the narrower carapace and in the absence of genal spines and subasaphine panderian organs; it differs from *Xenasaphus* in the bordering that is absent from the cephalon and usually absent from the pygidium; it differs from *Onchometopus* in the presence of basal lobes and vincular pits instead of the groove on the cephalon.

**Occurrence.** Baltoscandia; Lower–Middle Ordovician, Arenig–Caradoc.

*Asaphus expansus* (Wahlenberg, 1821)

Plate 2, figs. 1–5; Plate 21, fig. 9

*Entomostracites expansus*: Wahlenberg, 1821, p. 23 (cit. Brögger, 1882, p. 85).

*Asaphus expansus*: Dalman, 1828, p. 45, pl. 3, figs. 3a–3d; Angelin, 1854, p. 52, pl. 28, fig. 1; Brögger, 1882, p. 85, pl. 7, figs. 1–5; Schmidt, 1898, p. 19; 1901, p. 24, pl. 1, figs. 1, 2, and 5 (non fig. 3 = *A. lepidurus* Nieszkowski), pl. 12, fig. 6, figs. 1, 14–16; Lamanskii, 1905, p. 62; Jaanusson, 1956, pl. 1, figs. 1–5; Lesnikova and Weber, 1949, p. 285, pl. 68, figs. 6 and 7.

*Asaphus (Schizophorus) expansus*: Balashova, 1953, p. 391, pl. 1, figs. 8, 20, 32, pl. 2, fig. 14.

*Asaphus (Asaphus) expansus*: Jaanusson, 1953, p. 397; Balashova, 1976, p. 8; Nielsen, 1995, p. 77, figs. 60 and 61.

**Lectotype.** PIUU, no. Ög. 23, rolled carapace, designated and depicted by V. Jaanusson (1956, pl. 1, figs. 1–5), Heda (Öland Island); age and locality have not been mentioned.

**Diagnosis.** Cephalon shortened, lacking beaklike bend, glabella reaching anterior margin, basal lobes trapezoid, rudiments of glabellar lobes absent, occipital furrow deep, paradoublural furrows absent, cranidium frontally obtuse, marginal bend of anterior branch of facial suture rounded, eyes of medium length and height, distance between eyes and posterior margin much greater than its length, eye pedicles absent, eye lists poorly expressed, ocular area not elevated above shield and devoid of tubercles, occipital ring convex, pygidium shortened with rounded lateral margins and posterior end, rachis coarsely divided, terracelike folds sometimes present in anterior part of frontal lobe and absent from librigenae.

**Description.** The carapace is mainly medium-sized, sometimes large, the maximum measured width of the cephalon is 55 mm, the mean width is 36 mm. The cephalon is shortened (mean l/d is 0.44–0.45), rounded or, more rarely, weakly acuminate anteriorly, lacking a beaklike bend. The frontal lobe is moderately and strongly convex with the maximum convexity in its middle or posterior portion, reaching the anterior margin, not separated by the anterior furrow; its axial part is either smooth or bears a weakly expressed longitudinal ridge of a shallow pit. The medial lobe is clearly separated laterally, the flexure between it and the frontal lobe is narrow. The basal lobes are trapezoid. The glabellar lobe rudiments are absent. The eyes are

Explanation of Plate 2

**Fig. 1.** *Asaphus expansus gracilis* subsp. nov., holotype PIN, no. 4330/14, unrolled carapace,  $\times 1.5$ : (1a) cephalon, (1b) pygidium; left bank of the Volkhov River, village of Plekhanovo; Kunda Horizon, Volkhov Formation, upper part of the Khamontovo Member, lower part of the *expansus* Zone; collected by S.A. Mel'nikov.

**Fig. 2.** *Asaphus expansus* subsp. ind., specimen PIN, no. 4330/71, rolled carapace of juvenile specimen,  $\times 7$ : (2a) dorsal view, (2b) frontal view, (2c) side view; right bank of the Volkhov River abandoned quarry near the northern outskirts of the village of Simankovo; Kunda Horizon, Lynna Formation, Member 1, *expansus* Zone.

**Fig. 3.** *Asaphus expansus robustus* subsp. nov., holotype PIN, no. 4330/17, unrolled carapace,  $\times 1.5$ : (3a–3c) cephalon: (3a) dorsal view, (3b) frontal view, (3c) side view, (3d) pygidium; Lava River, Gorodishchenskii Kar'er outcrop; Kunda Horizon, Sillaoru Formation, Nikol'skoe Member, middle part of the *expansus* Zone.

**Figs. 4 and 5.** *Asaphus expansus deltifrons* subsp. nov.: (4) holotype PIN, no. 4330/19, cranidium superimposing pygidium,  $\times 1.5$ : (4a) view from the frontal lobe, (4b) frontal view, (4c) side view; right bank of the Volkhov River, village of Zapolek; Kunda Horizon, Lynna Formation, Member 2, upper part of the *expansus* Zone, 0–0.15 m below the roof of the member; (5) specimen PIN, no. 4330/70, cephalon,  $\times 2$ ; Putilovo outcrop; Kunda Horizon, Sillaoru Formation, Nikol'skoe Member, same age.

medium-sized and medium-high, placed away from the posterior margin at a distance considerably greater than their length, and moderately placed apart from each other (mean  $lo/l$ , 0.23–0.27; mean  $ho/lo$ , 0.79–0.84; mean  $la/lp$ , 1–1.1; and mean  $do/d$ , 0.55). The eye socles are fully developed. The ocular areas are not elevated above the carapace. The eye lists are distinct or unclear. The eye pedicles and tubercles on the posterolateral corners of the ocular areas are absent. The ocular bend of the anterior branch of the facial suture is absent, the marginal bend is rounded, and the anterior bend is nearly absent. The cranidium is obtuse frontally. The anterior part of the fixed gena is parallel-sided. The dorsal furrows are medium-deep or deep in the frontal lobe and distinct in the basal lobes. The glabellar furrows are deep. The pseudodorsal furrows are medium-deep. The occipital furrow is deep. The fossulae are not expressed. The paradoublural furrows are absent. The occipital node is distinct. The librigenae are weakly or strongly convex. The genal corners are rounded. The vincular pits are deep and are marked by a rather sharp bend in the lateral margin. The occipital ring and rings of the body rachis are convex. The pygidium is shortened (mean  $L/D$ , 0.53–0.54) and has rounded lateral and posterior margins. The rachis is coarsely segmented (seven to nine segments visible) and sharply or weakly bordered from behind. The pleura are weakly convex to convex, smooth, lacking a bordering behind the rachis. D-folds are as follows: coarse or weak (may be absent) on the anterolateral margins of the frontal lobe, weak on the posterior margin of the frontal lobe and on the medial and basal lobes, coarse on the occipital and rachial rings; on the pygidial rachis, they are either those accentuating segmentation or both those accentuating segmentation and intercalary, on the pleurae, they are only radial. The panderian organs are asaphine.

**Variability.** A juvenile specimen from the middle part of the Lynna Formation on the Volkhov River (Pl. 2, fig. 2) has the following characters of this species: the swollen glabella, trapezoid basal lobes, a deep occipital furrow and convex occipital ring; however, it differs in the very large and low eyes (relatively large eyes are characteristic of juvenile stages of asaphids), in the more attenuated cephalon and pygidium, and in the acuminate genal corners.

**Subspecies included.** *A. expansus expansus* (Wahlenberg, 1821), *A. expansus gracilis* subsp. nov., *A. expansus robustus* subsp. nov., and *A. expansus deltifrons* subsp. nov.

**Comparison.** This species is very close to *A. lepidurus*, from which it differs in the shorter cephalon and pygidium, more convex positive and more concave negative elements in the relief, absence of the cranial lingula, and in the clear eye lists. *A. khyrkoi* and *A. sulevi* have a cephalon that is similar to *A. expansus* in its shape. From those species, *A. expansus* differs in the shorter cephalon, in the trapezoid basal lobes, and in the deep occipital furrow; additionally, it differs from

*A. sulevi* in the absence of terracelike folds on its genae, in a more convex occipital ring, and in the shorter pygidium with a sharper subdivided rachis; from *A. khyrkoi*, it differs in the low, shorter eyes and in the terracelike folds on the frontal lobe of the glabella, which are usually poorly developed. This species is also similar to *A. kottukovi* in the general appearance of the cephalon and pygidium, deep occipital furrow, more convex occipital ring, and coarsely subdivided rachis of the pygidium but differs in the trapezoid basal lobes, shorter and lower eyes, absence of tubercles along the posterior margin of the eye area, and in the rounded marginal bend of the anterior branch of the facial suture. The comparison with *A. acuminatus* is given under the description of the latter.

**Remarks.** The specimen designated by Jaanusson (1956) as a lectotype of *A. expansus* possesses a set of characters, which separates it from representatives of this species from the Ladoga Region and from all individuals figured by Schmidt (1901) and Balashova (1953). These differences are of the same order as those that were used for separation of the *A. expansus* subspecies. The lectotype appears to belong to a separate subspecies, which is absent from the Ladoga Glint.

**Occurrence.** Lower Ordovician, Arenig, Kunda Horizon, *expansus* Zone; in the eastern part of the Ladoga Glint (Volkhov, Syas', and Lynna rivers): the Volkhov Formation (upper half of the Khamontovo Member) and Lynna Formation; in the western part of the Ladoga Glint and the Baltic Glint (west of the Volkhov River, at least to the village of Toila in Estonia): the Sillaoru Formation, Nikol'skoe Member. Outside of the Baltic–Ladoga Glint: Moscow Syncline (central part, Veksino Formation), Valdai Monocline (Obukhovo Formation) (Alikhova, 1960; Dmitrovskaia, 1991); southwestern Latvia (Kunda Horizon); Jelgava Depression (Ciecere Formation, Šakine Member, Baldone Formation, Špili and Ziemele members) (Ulst *et al.*, 1984); Sweden, Öland Island (Bohlin, 1949), Siljan Lake Region (Männil, 1966); Norway, Oslo Region, Huk Formation (Männil, 1966).

*Asaphus expansus expansus* (Wahlenberg, 1821)

*Asaphus expansus*: Jaanusson, 1956, pl. 1, figs. 1–5.

**Lectotype.** The type of the species.

**Diagnosis.** Cephalon slightly acuminate anteriorly; frontal glabellar lobe relatively weakly convex, with thin terracelike folds on its anterior side; palpebral lobes elevated above glabella; furrow of occipital part of cephalon relatively small.

**Comparison.** It differs from other subspecies in the anteriorly outlined pointing of the cephalon, less convex glabella, and weaker developed furrows of the occipital part of the cephalon.

**Occurrence.** Sweden, Öland Island (?).

*Asaphus expansus gracilis* subsp. nov.

Plate 2, fig. 1

**E t y m o l o g y.** From Latin *gracilis* (slender).

**H o l o t y p e.** PIN, no. 4330/14, carapace; Volkhov River, Plekhanovo village; Kunda Horizon, Volkhov Formation, upper part of the Khamontovo Member, lower part of the *expansus* Zone (collected by S.A. Mel'nikov) (Pl. 2, fig. 1).

**D i a g n o s i s.** Cephalon somewhat obtuse anteriorly; frontal lobe moderately convex, with maximum convexity in anterior or central part, without terracelike folds; palpebral lobes elevated above glabella; occipital furrows relatively small.

**C o m p a r i s o n.** It differs from other subspecies in the absence of terracelike folds on the anterior side of the frontal lobe; additionally, from *A. expansus robustus* and *A. expansus deltifrons*, in the less convex glabella.

**O c c u r r e n c e.** Lower Ordovician, Arenig, Kunda Horizon, *expansus* Zone. Eastern part of the Ladoga Glint: the Volkhov Formation, the upper part of the Khamontovo Formation and the lower part of the first member of the Lynna Formation; western part of the Ladoga Glint: the Sillaoru Formation, the lower fineoolitic part of the Nikol'skoe Member.

**M a t e r i a l.** Forty-five specimens from the Syas' River, the Volkhov River, village of Zvanka (0.05–0.25 m above ds2 or 1.8–2 m below ds3), in quarries between the villages Simankovo and Obukhovo (0.1–0.3 m above ds2 or 2.2–2.4 m below ds3); Lava River; quarries near the village of Putilovo.

*Asaphus expansus robustus* subsp. nov.

Plate 2, fig. 3

*Asaphus expansus*: Schmidt, 1901, p. 24, pl. 1, figs. 1, 2; pl. 12, fig. 6; figs. 14–16; Lesnikova and Weber, 1949, p. 285, pl. 68, figs. 6 and 7.

*Asaphus (Schizophorus) expansus*: Balashova, 1953, p. 391, pl. 2, fig. 14.

*Asaphus (Asaphus) expansus*: Nielsen, 1995, p. 77, fig. 60, A, F, G, J, K (non C, D – ?).

**E t y m o l o g y.** From Latin *robustus* (robust).

**H o l o t y p e.** PIN, no. 4330/17, carapace; Lava River, Gorodishchenskii Kar'er outcrop (Fig. 5); Kunda Horizon, Sillaoru Formation, Nikol'skoe Member, middle part of the *expansus* Zone (Pl. 2, fig. 3).

**D i a g n o s i s.** Cephalon shortened, anteriorly obtuse; frontal lobe convex with maximum convexity in its middle part; thin terracelike folds observable on anterior side of frontal lobe; palpebral lobes elevated above glabella; occipital furrows deep.

**C o m p a r i s o n.** From *A. expansus expansus* and *A. expansus gracilis*, this subspecies differs in the greater convexity of the cephalon and glabella and better expressed furrows; additionally, it occasionally differs in the presence of terracelike folds on the anterior side of the frontal lobe from the latter subspecies and from *A. expansus deltifrons*, in the palpebral lobes being elevated above the glabella.

**O c c u r r e n c e.** Lower Ordovician, Arenig, Kunda Horizon, middle part of the *expansus* Zone; eastern part of the Ladoga Glint: Lynna Formation, Member 1; western part of the Ladoga Glint (west of the Volkhov River): Sillaoru Formation, lower and middle parts of the Nikol'skoe Member.

**M a t e r i a l.** Two hundred and twenty-seven specimens: Syas' River Basin; Lynna River mouth, 0.75–2.2 m above ds2 or 0.65–2.1 m below ds3; the Volkhov River, in quarries between the villages Simankovo and Obukhovo, 0.4 m above ds2 or 2.1 m below ds3, near the village of Plekhanovo, 1.65 m above ds2 or 0.7 m below ds3, village of Zvanka, 1.15–1.25 m above ds2 or 0.8–0.9 m below ds3; quarry 2 km westward of the village of Voibokalo, 0.22–0.3 m above ds2; Lava River, 0.05–0.25 m above ds2 or 0.57–0.37 m below ds3; village of Putilovo, 0.15 m above ds2 or 0.35 m below ds3.

*Asaphus expansus deltifrons* subsp. nov.

Plate 2, figs. 4 and 5

*Asaphus expansus*: Dalman, 1828, pl. 3, figs. 3a–3d; Brögger, 1882, pl. 7, figs. 1 and 2.

**E t y m o l o g y.** From Greek *delta* (name of letter) and Latin *frons* (frons).

**H o l o t y p e.** PIN, no. 4330/19, cranidium and pygidium; Volkhov River, village of Zapolek; Kunda Horizon, Lynna Formation, series 2–0.15 m below the roof, upper part of the *expansus* Zone (Pl. 2, fig. 4).

**D i a g n o s i s.** Cephalon slightly obtuse anteriorly; frontal lobe so convex that its posterior part is elevated above the palpebral lobes; coarse terracelike folds developed on the anterior side of glabella; occipital furrows deep.

**C o m p a r i s o n.** From other subspecies, it differs in the stronger convex frontal lobe of the glabella and the lower (below the level of the glabella) position of the palpebral lobes.

**O c c u r r e n c e.** Lower Ordovician, Arenig, Kunda Horizon, upper part of the *expansus* Zone; eastern part of the Ladoga Glint: Lynna Formation, upper part of Member 1 and Member 2; western part of the Ladoga Glint: Sillaoru Formation, upper part of the Nikol'skoe Member.

**M a t e r i a l.** Forty-seven specimens: Lynna River, 2.5 m above ds2 or 0.35 m below ds3; Volkhov River, village of Zvanka, 1.7–1.95 m above ds2 or 0.1–0.35 m below ds3, village of Stuglevo, 0.1 m below ds3, village of Plekhanovo, 1.8–2.15 m above ds2 or 0.2–0.55 m below ds3, abandoned quarries between the villages Simankovo and Obukhovo, 1.5–1.9 m above ds2 or 0.6–1 m below ds3; quarry 2 km west of the village of Voibokalo; Lava River, 0.4–0.62 m above ds2 or 0–0.22 m below ds3; village of Kikol'shchina, 0.4 m above ds2 or 0.15 m below ds3; quarries near the village of Putilovo, 0.4–0.45 m above ds2 or approximately 0.1 m below ds3.

*Asaphus lepidurus* Nieszkowskii, 1859

Plate 1, figs. 1–7; Plate 13, fig. 6; Plate 21, figs. 1 and 12

*Asaphus lepidurus*: Nieszkowskii, 1859, p. 360; Schmidt, 1901, p. 29, pl. 1, figs. 4, 6, 7, pl. 12, fig. 7, text-figs. 17–19; Lamanskii, 1905, p. 62; Lesnikova and Weber, 1949, p. 285, pl. 68, figs. 3 and 4.

*Asaphus expansus* var. *lepidura*: Schmidt, 1898, p. 19.

*Asaphus expansus*: Schmidt, 1901, pl. 1, fig. 3.

*Asaphus (Schizophorus) lepidurus*: Balashova, 1953, p. 389, pl. 1, fig. 3, pl. 2, fig. 3.

*Asaphus (Asaphus) lepidurus*: Jaanusson, 1953a, p. 397; Balashova, 1976, p. 8; Nielsen, 1995, p. 81, figs. 63 and 64.

**N**o t y p e. DPStPSU, no. 593/9243, unrolled carapace, designated and depicted by Balashova (1953, pl. 2, fig. 3); right bank the Volkhov River upstream of the village of Obukhovo; 3.8 m below the floor of the lower lenticular bed, BIIγ[<sub>sub</sub>]. The number indicated in the cited paper does not correspond to the label of the specimen.

**D**i a g n o s i s. Cephalon of medium proportions, sometimes with beaklike bend; glabella terminating far from anterior end; basal lobes trapezoid; rudiments of glabellar lobes absent; occipital furrow deep; paradoublural furrows absent or just outlined; cranidium with broad lingula; marginal bend of anterior branch of facial suture rounded; eyes medium-long and medium-high, predominantly equidistant from anterior and posterior ends of cephalon; eye pedicles absent; eye lists absent; ocular areas not elevating above cephalon, devoid of tubercles; occipital ring convex; pygidium of medium proportions, with rounded lateral margins and posterior end; rachis coarsely subdivided; terracelike folds absent from anterior side of frontal lobe and occasionally present on librigenae.

**D**e s c r i p t i o n. The carapace is predominantly medium-sized, the maximum measured width of the cephalon is 58 mm, the mean width is 40 mm. The cephalon is of medium proportions (mean l/d is 0.5), acuminate anteriorly, having a weak beaklike bend or lacking it. The frontal lobe is moderately convex, with the maximum convexity in its middle part, not reaching far into the anterior margin, separated from the latter by a weak furrow and possessing a weak longitudinal ridge. The medial lobe is well-defined laterally, the flexure between it and the frontal lobe is sharp. The basal lobes are trapezoid, well-expressed. The rudiments of the glabellar lobes are usually absent or visible as small depressions of the carapace, which are emphasized by series of thin terracelike folds. The eyes are medium-long, medium-high, and situated in the center, but may be approximated to the posterior as well as to the anterior margins and are moderately spaced apart from each other (mean lo/l, 0.26; mean ho/lo, 0.82; mean la/lp, 1.1; mean do/d; 0.55). The eye socles are fully developed. The ocular areas are not elevated above the carapace. The eye lists, eye pedicles and tubercles in the posterolateral corners of the ocular areas are absent. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded, and the anterior bend is

distinct. The cranidium has a wide lingula. The distance between the facial sutures at the level of the marginal bends is greater than the distance between them at the eye socles. The maximum width of the anterior part of the fixed gena is near the fossulae. The dorsal furrows are medium-deep in the frontal lobe, small and distinct in the basal lobes. The glabellar furrows are deep. The pseudodorsal furrow are medium-deep. The occipital furrow is deep. The fossulae are unclear. The paradoublural furrows are absent or weakly defined. The occipital node is distinct. The librigenae are flat, the genal corners are acuminate. The vincular pits are deep and marked by a weak or rather sharp curvature of the lateral margin. The occipital ring is convex. The rings of the body rachis are convex. The pygidium is medium proportional (mean L/D is 0.58), having rounded lateral and posterior margins. The rachis is coarsely divided (seven or eight segments are visible on its carapace) and weakly bordered from behind. The pleurae are weakly convex, smooth, lacking bordering behind the rachis. The following D-folds are present: weak folds on the posterior part of the frontal lobe, on the medial and basal lobes, rarely in the posterolateral corner of the ocular area; coarse and frequent on the occipital ring and rachial rings of the body; emphasizing segmentation and intercalary rings on the pygidial rachis; transverse and radial rings on the pygidial pleurae. The panderian organs are asaphine.

**V**a r i a b i l i t y. This species is much variable. The relative width of the cephalon, the degree of its acuteness, development of the beaklike bend, eye lists, vincular pits, eye size and their position on the cephalon, furrow depth, sharpness of the segmentation of the pygidial rachis, and expression of the terracelike folds are varying.

A form occurring in abundance in the Lynna River section, 1.6 m above the floor of the Frizy Member, is very distinctive. It is characterized by large eyes approximated to the anterior margin, a shortened cephalon and pygidium, and rather coarsely segmented pygidial rachis (Pl. 1, fig. 2).

The age variability is expressed in the enlargement of the relative width of the carapace during the last ontogenetic stages.

**C** o m p a r i s o n. This species is similar to *A. expansus* in both its morphology and its position in sections; a comparison has been provided above.

From the stratigraphically close *A. ? broeggeri*, it differs in the greater concavity of negative elements and greater convexity of positive elements of the carapace, in higher eyes, and in the segmentation of the pygidial rachis. *A. raniceps*, *A. acuminatus*, *A. striatus*, *A. ingrianus*, *A. laevissimus*, middle-sized individuals of *A. plautini*, *A. holmi* (low-eye form), and *A. bottnicus* are close to *A. lepidurus* in the general shape of the cephalon and in the medium height of the eyes. From all these species, the latter species differs in the trapezoid basal lobe, deep occipital furrow, and convex

occipital ring. Additionally, it differs from *A. raniceps* and *A. acuminatus* in all the furrows being better developed and in the coarsely segmented pygidial rachis, also from *A. acuminatus*, it differs in generally larger eyes, from *A. striatus*, in shorter eyes, from *A. ingri-anus*, *A. plautini*, *A. holmi*, and *A. bottnicus*, in the absence of terracelike folds on the anterior part of the frontal lobe, from *A. plautini*, in shorter eyes and paradoublural furrows, in the absence of traces of tubercles from the ocular areas, in the shorter pygidium possessing a coarsely segmented rachis, and from *A. holmi*, in having smaller eyes, shallower paradoublural furrows, in the absence of tubercles from the ocular areas and terracelike folds from the genae, and in the pygidium having rounded lateral margins and a posterior end.

**Remarks.** Considerable morphologic variability and relatively wide vertical distribution suggest that we are dealing with a group of close forms of subspecific or even specific rank, instead of a single species. All attempts to separate them face the following difficulties: (1) the characters are variable, (2) the quantity and preservation of material coming from different levels and different sections are highly unequal, (3) the majority of samples come from the upper part of the Frizy Member; however, it is unclear whether or not this level is synchronous in different sections. The designation of the lectotype and holotype by Balashova (1953, 1976), who used the specimen depicted by Schmidt (1901, pl. 2, figs. 7, 7a), is not valid, since that specimen does not belong to *Nieszkowskii*'s originals.

**Occurrence.** Lower Ordovician, Arenig, Volkhov Horizon, beds with *A. lepidurus*; Volkhov Formation, Frizy and lower half of the Khamontovo Member.

**Material.** Two hundred and fifty specimens: Syas' River, Lynna River mouth, 0.55–3 m above the Zheltyaki roof or 0.45–2.9 m below ds2; Volkhov River, village of Babino, 3–4.4 m above the Dikari roof or 0.55–1.95 m below ds2; quarry 2 km west of the station of Voibokalo, 0.35–0.5 m below ds2; Lava River, 3.65–4.3 m above the Dikari roof or 0.4–1.05 m below ds2; village of Nikol'shchina, 0.25 m below ds2; village of Putilovo, 3.55–4.15 m above the Dikari roof or 0.7–1.3 m below ds2.

*Asaphus acuminatus* Boeck, 1838

Plate 3, figs. 1–5; Plate 4, fig. 4; Plate 21, fig. 3

*Asaphus acuminatus*: Boeck, 1838, p. 142 (cit. Brögger, 1882); Angelin, 1854, p. 53, pl. 28, figs. 2, 2a–2c, pl. 29, fig. 2; Brögger, 1882, p. 93, pl. 8, figs. 5a and 5b; Lamanskii, 1905, p. 62.

*Asaphus raniceps*: Schmidt, 1901, pl. 1, figs. 9–11, pl. 2, figs. 1–3; Lesnikova and Weber, 1949, pl. 68, figs. 8 and 9.

*Asaphus raniceps* var. *lamanskii*: Schmidt, 1901, p. 35, pl. 12, figs. 8–10, text-fig. 21.

*Asaphus lamanskii*: Lamanskii, 1905, p. 62.

*Asaphus (Asaphus) raniceps* var. *lamanskii*: Jaanusson, 1953a, p. 397.

*Asaphus (Schizophorus) acuminatus*: Balashova, 1953, p. 394, pl. 1, fig. 4, pl. 5, fig. 3.

*Asaphus (Schizophorus) lamanskii*: Balashova, 1953, p. 392, pl. 1, fig. 33, pl. 2, fig. 7, pl. 5, figs. 9 and 10.

*Asaphus (Schizophorus) raniceps*: Balashova, 1953, pl. 1, fig. 5.

*Asaphus (Asaphus) lamanskii*: Balashova, 1976, p. 9.

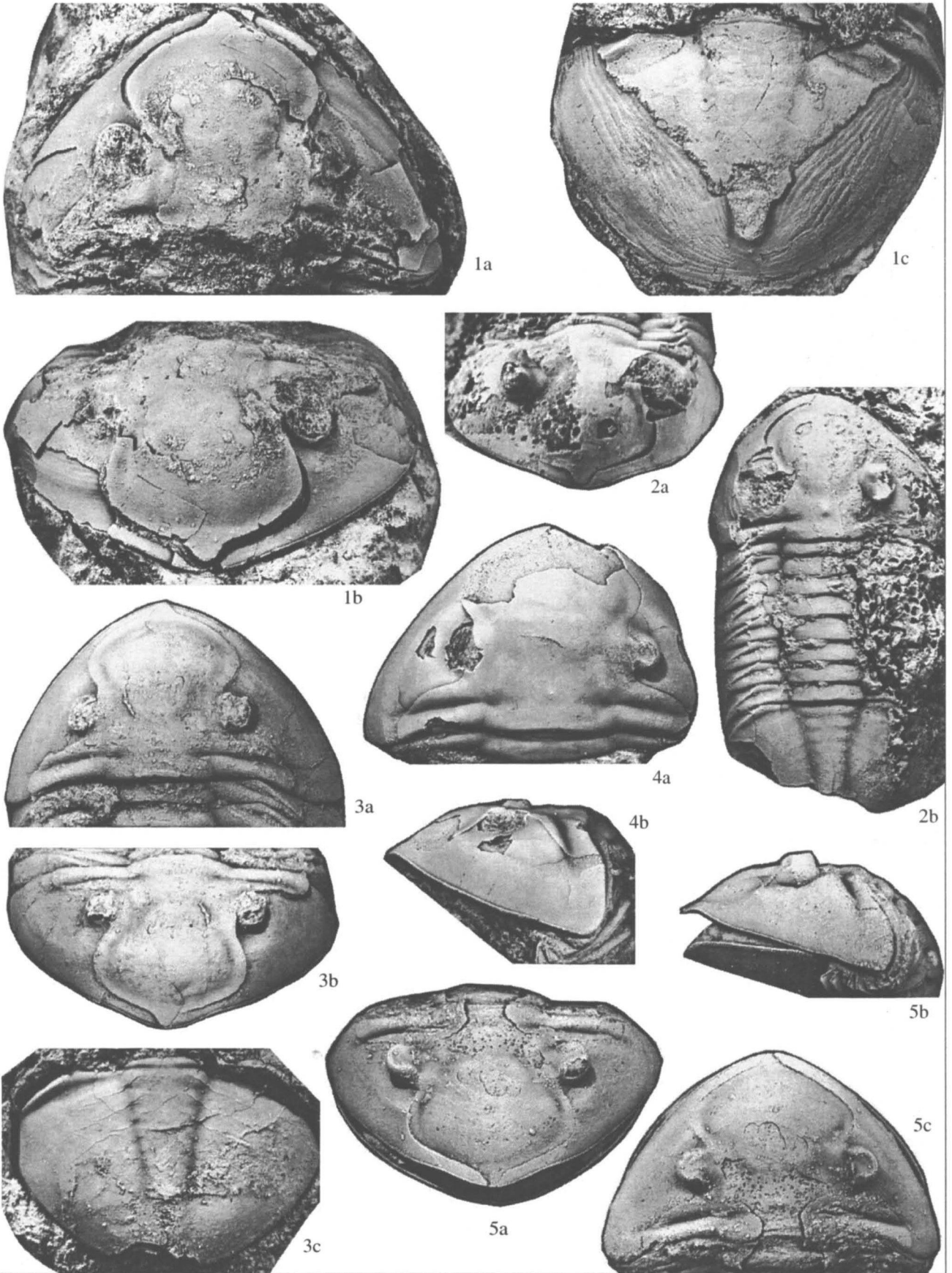
*Asaphus (Asaphus) acuminatus*: Nielsen, 1995, p. 84, fig. 66, A–G, I–J (non fig. 66 H – ?); fig. 67, A–C, E–I (non fig. 67 D – *Megistaspis* (?)); fig. 68.

*Asaphus (Asaphus) incertus*: Nielsen, 1995, figs. 74a–74c.

**Lectotype.** – PMO, no. 2021, deformed and partially destroyed carapace, depicted by Brögger (1882, pl. 8, figs. 5a, 5b), designated by Nielsen (1995); Norway, Oslo Region; *Orthoceras* Limestone.

**Diagnosis.** Cephalon elongated, with sharp beaklike bend; glabella not reaching far into the anterior margin; basal lobes lenslike; rudiments of glabellar lobes present; occipital furrow shallow, developed along its entire length or as a pit; paradoublural furrows absent; cranidium with long, wide or narrow lingula; marginal bend of anterior branch of facial suture rounded; eye very short, medium-high, distance between them and posterior margin greater than their length; eye pedicles absent; eye lists absent; ocular areas not elevated above cephalon and devoid of tubercles; occipital ring flat; pygidium elongated, with rounded lateral margins and rounded or slightly acuminate posterior end; rachis weakly divided; anterior part of frontal lobe and librigenae barren of terracelike folds.

**Description.** The carapace is medium-sized or large. The cephalon is elongated, acuminate anteriorly, having a sharp beaklike bend. The frontal lobe is medium to weakly convex, with the maximum convexity in the middle part, not reaching far into the anterior margin, bordered anteriorly with a weak or rather sharp furrow, and bearing a longitudinal ridge. The medial lobe is weakly bordered laterally, the flexure between it and the frontal lobe is weak. The basal lobes are lenslike, distinctly expressed. Rudiments of the glabellar lobes are present. The eyes are short and very short, medium-high, moderately separated, the distance between them and the posterior margin is greater and much greater than their length (however, they are closer to the posterior margin than to the anterior one). The eye socle are fully developed. The ocular areas are not elevated above the cephalon. The eye pedicles, lists, and tubercles in the posterolateral corners of the ocular areas are absent. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded, and the anterior bend is distinct. The cranidium possesses a narrow or wide, long lingula. The distance between the facial sutures at the level of the marginal bends is greater than such a distance at the eye socles. The dorsal furrows are shallow to medium-deep on the frontal lobe and shallow and weakly expressed on the basal lobes. The glabellar furrows are shallow. The pseudodorsal furrows are shallow and unclear. The occipital furrow is either shallow and developed along its entire length or developed as a pit. The fossulae are either absent or clear. The paradoublural furrows are absent. The occipital node is



distinct. The librigenae are flat. The genal corners are acuminate. The vincular pits are weakly developed, not expressed on the outer surface. The occipital ring is flat. The rings of the body rachis are flat to weakly convex. The pygidium is elongated, with rounded lateral margins and a rounded or slightly acuminate posterior margin. The rachis is weakly subdivided (two or three segments are visible on the outer face of the carapace) and weakly bordered from behind. The pleurae are flattened, smooth, without a bordering behind the rachis. The vincular tubercles are present. The following D-folds are present: weak and rare on the rings of the body rachis, radial and rare transverse on the pygidial pleurae and weak, underlining segmentation and intercalary on the rachis. The panderian organs are asaphine.

**Variability.** Similarly to *A. raniceps*, the variability is expressed in forms with an elongated cephalon and pygidium, with a smoothed carapace and shortened shields, and with more strongly expressed furrows.

**Subspecies included.** *A. acuminatus acuminatus* Boeck and *A. acuminatus lamanskii* Schmidt.

**Comparison.** Similar to *A. raniceps* and *A. striatus* in the elongated and acuminate shape of the cephalon, in the more weakly defined furrows, and in the lenslike basal lobes. The main differences from *A. raniceps* are the following: an expressed segmentation of the pygidial rachis, the presence of terracelike folds on the latter, sporadically shorter eyes, a narrower and longer lingula of the cranidium, and a stronger developed beaklike bend of the anterior margin of the cephalon. From *A. striatus*, it plainly differs in having shorter eyes, in the frontal glabellar lobe being bordered anteriorly, the long lingula of the cranidium, and in the beaklike bend of the anterior margin of the cephalon. From *A. ? broeggeri*, it differs in the basal lobes being distinct and in the pygidial rachis being subdivided. From *A. expansus*, which occurs in association with *A. acuminatus*, the latter species differs in the majority of characters. The comparison with *A. lepidurus* is given under the description of the latter species.

**Occurrence.** Ladoga Glint, Southern Sweden, Norway; Middle Ordovician, Llanvirn, Kunda Horizon, *expansus* Zone.

#### *Asaphus acuminatus acuminatus* Boeck, 1838

Plate 3, figs. 1 and 2; Plate 4, fig. 5

*Asaphus acuminatus*: Boeck, 1838, p. 142 (cit. Brögger, 1882); Angelin, 1854, p. 53, pl. 28, fig. 2, pl. 29, fig. 2 (non pl. 28, fig. 2a, 2b (= *A. acuminatus lamanskii*)); Brögger, 1882, p. 93, pl. 8, figs. 5a and 5b; Lamanskii, 1905, p. 62.

*Asaphus (Asaphus) acuminatus*: Nielsen, 1995, p. 84, fig. 66A–G, I–J (non fig. 66H – ?); fig. 67A–C, E–I (non fig. 67D – *Megistaspis* (?)); fig. 68.

*Asaphus (Asaphus) incertus*: Nielsen, 1995, fig. 74a.

**Lectotype.** The type of the species.

**Diagnosis.** Eyes medium-sized, lingula of cranidium wide and long.

**Measurements (mm) and ratios:** maximum measured width of cephalon, 53 mm; mean l/d, 0.55; mean lo/l, 0.23; mean ho/lo, 0.71; mean la/lp, 1.4; mean do/d, 0.57; and mean L/D, 0.64.

**Comparison** is given under the description of *A. acuminatus lamanskii*.

**Occurrence.** Middle Ordovician, Llanvirn, Kunda Horizon, upper part of the *expansus* Zone (with *A. expansus deltifrons*); eastern part of the Ladoga Glint, Lynna Formation, Member 2, lower part of the Sillaoru Formation; western part of the Ladoga Glint, Sillaoru Formation, upper part of the Nikol'skoe Member. Outside the Ladoga Glint: Baltic Glint, Sillaoru Formation, upper part of the Nikol'skoe Member; Norway, Oslo Graben, Huk Formation, 3cβ–γ; southern Sweden (Nielsen, 1995).

**Material.** One hundred and thirty-two specimens: Lynna River, 0.1–0.35 m below ds3 or 2.50–2.75 m above ds2; Volkhov River, village of Zvanka, 0.1–0.35 m below ds3 or 1.6–2.05 m above ds2, village of Plekhanovo, 2.1–2.3 m above ds2, village of Obukhovo, 2.3–2.65 m above ds2; quarry near the station of Voibokalo.

#### *Asaphus acuminatus lamanskii* F. Schmidt, 1901

Plate 3, figs. 3–5; Plate 21, fig. 3

*Asaphus acuminatus*: Angelin, 1854, p. 53, pl. 28, figs. 2a and 2b.

*Asaphus raniceps* var. *lamanskii*: Schmidt, 1901, p. 35, pl. 12, figs. 8–10, text-fig. 21.

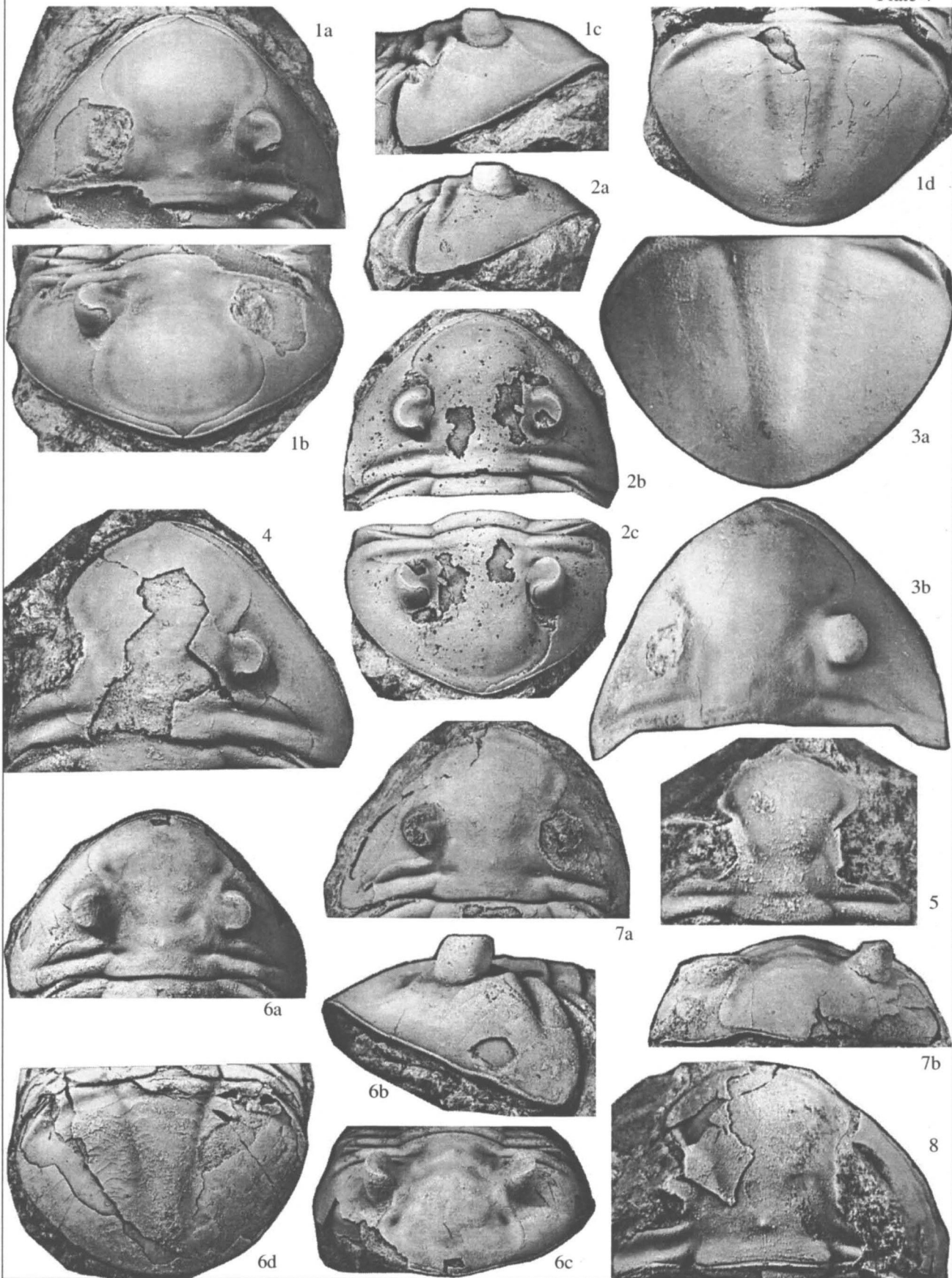
*Asaphus raniceps*: Schmidt, 1901, pl. 1, figs. 9–11, pl. 2, figs. 1–3, text-fig. 2; Lesnikova and Weber, 1949, pl. 68, figs. 8 and 9.

*Asaphus acuminatus*: Schmidt, 1901, pl. 2, fig. 1; Lamanskii, 1905, p. 62.

#### Explanation of Plate 3

**Figs. 1 and 2.** *Asaphus acuminatus acuminatus* Boeck, 1838: (1) specimen PIN, no. 4330/20, unrolled partly destroyed carapace,  $\times 1.5$ : (1a, 1b) cephalon: (1a) dorsal view, (1b) view from the frontal lobe, (1c) pygidium imprint; right bank of the Volkhov River, village of Stuglevo; Kunda Horizon, Lynna Formation, Member 2, upper part of the *expansus* Zone; (2) specimen PIN, no. 4330/22, unrolled, corroded and partially destroyed carapace: (2a) cephalon, view from the frontal lobe,  $\times 1.7$ . (2b) general appearance,  $\times 1.5$ ; Voibokalo outcrop; Kunda Horizon, Sillaoru Formation, Nikol'skoe Member, same age.

**Figs. 3–5.** *Asaphus acuminatus lamanskii* F. Schmidt, 1901: (3) specimen PIN, no. 4330/13, bend carapace,  $\times 1.5$ : (3a, 3b) cephalon: (3a) dorsal view, (3b) view from the frontal lobe, (3c) pygidium; left bank of the Volkhov River, village of Plekhanovo; Kunda Horizon, Lynna Formation, Member 1, lower part of the *expansus* Zone, talus; (4) specimen PIN, no. 4330/12, cephalon,  $\times 1.5$ : (4a) dorsal view, (4b) side view; left bank of the Syas' River, about 1 km upstream of the Lynna River mouth; Kunda Horizon, Volkhov Formation, upper part of the Khamontovo Member, same age, talus; (5) specimen PIN, no. 4330/72, rolled carapace,  $\times 1.5$ : (5a) view from the frontal lobe, (5b) side view, (5c) dorsal view; left bank of the Volkhov River, abandoned quarry near the village of Izviz; Kunda Horizon, Lynna Formation, Member 1, same age, talus.



*Asaphus lamanskii*: Lamanskii, 1905, p. 62; Lesnikova and Weber, 1949, p. 285, pl. 68, figs. 8 and 9, pl. 69, fig. 2.

*Asaphus (Asaphus) raniceps* var. *lamanskii*: Jaanusson, 1953a, p. 397.

*Asaphus (Schizophorus) lamanskii*: Balashova, 1953, p. 392, pl. 1, fig. 33, pl. 2, fig. 7, pl. 5, figs. 9–10.

*Asaphus (Schizophorus) acuminatus*: Balashova, 1953, p. 394, pl. 1, fig. 4, pl. 5, fig. 3.

*Asaphus (Schizophorus) raniceps*: Balashova, 1953, pl. 1, fig. 5.

*Asaphus (Asaphus) lamanskii*: Balashova, 1976, p. 9.

*Asaphus (Asaphus) incertus*: Nielsen, 1995, figs. 74b and 74p.

**Lectotype.** Specimen depicted by Schmidt (1901, pl. 12, fig. 8) and designated by Balashova (1976); Volkhov River; substage B<sub>2</sub>b; specimen lost. Paralectotypes GMAGI, nos. 13, 14, 15, 17/11152 and PIN, nos. 4248/7, 91; all specimens came from the Volkhov River, near the villages of Izvoz and Obukhovo; substages B<sub>2</sub>b–B<sub>3</sub>a.

**Diagnosis.** Eyes very short, relative length of palpebral lobes minimal among all species, lingula of cranium narrow and long.

**Measurements (mm) and ratios:** maximum measured width of cephalon, 44.5; mean d, 37.5; mean lo/l, 0.21; mean ho/lo, 0.82; mean la/lp, 1.3; mean do/d, 0.54; and mean L/D, 0.62.

**Comparison.** Differs from *A. acuminatus* in the eyes being shorter and in the narrower lingula of the cranium.

**Remarks.** An explanation as to why the neotype designated by Balashova (1953) is invalid is given in the introductory part of Systematic Paleontology.

**Occurrence.** Middle Ordovician, Llanvrim, Kunda Horizon, lower part of the *expansus* Zone (with *A. expansus gracilis* and *A. expansus robustus*); eastern part of the Ladoga Glint, Volkhov Formation, upper part of the Khamontovo Formation and Lynna Formation, Member 1; western part of the Ladoga Glint, Sillaoru Formation, lower and middle parts of the Nikol'skoe Formation.

**Material.** Sixty-one specimens: Syas' River; Volkhov River, village of Zvanka, 0.85 m below ds3 or 1.2 m above ds2, talus of Member 1 of the Lynna Formation; quarry 2 km west of the village of Voibokalo, 0.18 m above ds2 or 0.4 m below ds3; Lava River, 0.37 m

above ds2 or 0.25 m below ds3; village of Putilovo, 0.1–0.18 m above ds2 or 0.32–0.4 m below ds3.

#### *Asaphus raniceps* Dalman, 1828

Plate 4, figs. 1–4; Plate 21, figs. 2 and 11

*Asaphus expansus* var.  $\beta$  *raniceps*: Dalman, 1828, pl. 3, fig. 4.

*Asaphus raniceps*: Angelin, 1854, p. 53, pl. 28, fig. 2; Brögger, 1882, p. 92; Schmidt, 1901, p. 32, pl. 1, fig. 8, text-fig. 20 (non pl. 1, figs. 9–11, pl. 2, figs. 1–3 = *A. acuminatus lamanskii* F. Schmidt); Lamanskii, 1905, p. 62; Lesnikova and Weber, 1949, p. 285, pl. 68, fig. 5, pl. 69, figs. 3a and 3b.

*Asaphus major*: Lamanskii, 1905, p. 63.

*Asaphus (Asaphus) "raniceps"*: Jaanusson, 1953a, p. 394; Nielsen, 1995, p. 96.

*Asaphus (Schizophorus) raniceps*: Balashova, 1953, p. 395, pl. 1, fig. 23, pl. 2, fig. 4 (non pl. 1, fig. 5 = *A. acuminatus lamanskii* F. Schmidt).

*Asaphus (Schizophorus) major*: Balashova, 1953, p. 396, pl. 1, fig. 6, pl. 2, fig. 5.

*Asaphus (Asaphus) raniceps*: Balashova, 1976, p. 9.

**Neotype.** GMAGI, no. 16/11152, unrolled carapace, depicted by Schmidt (1901, p. 35, fig. 20), designated here (pl. 4, fig. 3); village of Nikol'shchina; substages B<sub>2</sub>b–B<sub>3</sub>a. The stratigraphic position of the specimen written on the original label encompasses the upper part of the Volkhov Formation and the Sillaoru Formation; however, most probably, it comes from the lower part of the Obukhovo Formation.

**Diagnosis.** Cephalon elongated, with sharp beaklike bend; glabella not reaching anterior margin; basal lobes lenslike; rudiments of glabellar lobes present; occipital furrow absent; paradoublural furrows absent; cranium with wide short lingula; marginal bend of anterior branch of facial suture rounded; eyes medium long and high, distance between them and posterior margin slightly greater than their length; eye pedicles absent; eye lists absent; ocular areas not elevated above cephalon and devoid of tubercles; occipital ring flat; pygidium elongated, with rounded lateral margins and rounded or slightly acuminate posterior end; rachis undivided; terracelike folds absent from anterior part of frontal lobe and librigenae.

#### Explanation of Plate 4

**Figs. 1–4.** *Asaphus raniceps* Dalman, 1828: (1) specimen PIN, no. 4330/25, unrolled carapace,  $\times 1.5$ : (1a–1c) cephalon: (1a) frontal view, (1b) view from the frontal lobe, (1c) side view, (1d) pygidium; Lava River, Gorodishchenskii Kar'er outcrop; Kunda Horizon, Obukhovo Formation, Member 1, lower part of the *raniceps*–*striatus* Zone, 0–0.15 m above the floor of the formation; (2) specimen PIN, no. 4330/26, cephalon,  $\times 1.5$ : (2a) lateral view, (2b) dorsal view, (2c) view from the frontal lobe; abandoned quarry south of the village of Putilovo; Kunda Horizon, Obukhovo Formation, Member 1, same age, 0.05 m above the floor of the formation; (3) neotype GMAGI, no. 16/11152, unrolled, partially deformed carapace,  $\times 1.5$ : (3a) pygidium, (3b) cephalon; environs of the village of Putilovo, village of Nikol'shchina; substages B<sub>2</sub>b–B<sub>3</sub>a; (4) specimen PIN, no. 4330/24, cephalon with left librigena missing,  $\times 1.5$ ; right bank of the Volkhov River, village of Zapolek; Kunda Horizon, Obukhovo Formation, Member 1, lower part of the *raniceps*–*striatus* Zone, 0.05 m above the floor of the formation.

**Fig. 5.** *Asaphus acuminatus acuminatus* Boeck, 1838, specimen PIN, no. 4330/73, cranium of small individual,  $\times 4$ ; right bank of the Volkhov River, abandoned quarry between the villages of Simankovo and Obukhovo; Kunda Horizon, Lynna Formation, Member 2, upper part of the *expansus* Zone.

**Figs. 6–8.** *Asaphus striatus sarsi* Brögger, 1882: (6) specimen PIN, no. 4330/27, unrolled carapace: (6a–6c) cephalon: (6a) dorsal view,  $\times 1$ , (6b) side view,  $\times 1.5$ , (6c) view from the frontal lobe,  $\times 1$ , (6d) pygidium,  $\times 1$ ; Putilovo outcrop; Kunda Horizon, Obukhovo Formation, Member 3, middle part of the *raniceps*–*striatus* Zone, talus; (7) specimen PIN, no. 4330/29, cephalon,  $\times 1$ : (7a) dorsal view, (7b) frontal view; same age and locality; (8) specimen PIN, no. 4330/77, imprint of cranium of juvenile individual,  $\times 3$ ; same age and locality.

**Description.** The carapace is medium-sized and large, the maximum measured width of the cephalon is 54 mm, mean d, 46.5 mm. The cephalon is elongated (mean l/d, 0.54), anteriorly acuminate, with a sharp beaklike bend. The frontal lobe is weakly convex, with the maximum convexity in its middle part, not reaching the anterior margin, bordered anteriorly with a weak or rather clear furrow, and bearing a longitudinal ridge. The medial lobe is weakly bordered laterally, the flexure between it and the frontal lobe is weak. The basal lobes are lenslike and distinct. Rudiments of the glabellar lobes are present. The eyes are medium-long and medium-high, approximated to the posterior end at a distance, which is a little greater than their length, and are moderately separated (mean lo/l, 0.25; mean ho/lo, 0.78; mean la/lp, 1.5; and mean do/d, 0.55). The eye socles are fully developed. The ocular areas are not elevated above the cephalon. The eye pedicles, eye lists, and tubercles in the posterolateral corners of the ocular areas are absent. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded, and the anterior bend is distinct. The cranidium has a wide and short lingula. The distance between the facial sutures at the level of the marginal bends is greater than such distance at the eye socles. The anterior part of the librigena is parallel-sided. The dorsal furrows of the frontal lobes are medium-deep, those of the basal lobes are shallow and poorly defined. The glabellar furrows are shallow. The pseudodorsal furrows are shallow and unclear. The occipital furrow is absent. The fossulae are unclear or not expressed. The paradoublural furrows are absent. The occipital node is distinct. The librigenae are flat. The genal corners are acuminate. The vincular pits are weakly developed and not expressed on the outer face. The occipital ring and the rings of the body rachis are flat. The pygidium is elongated (mean L/D, 0.65), with rounded lateral margins and a rounded or slightly acuminate posterior margin. The rachis is smooth and weakly bordered from behind. The pleurae are flattened, smooth, and lack bordering behind the rachis. The vincular tubercles are absent. The following D-folds are present: weak and rare on the rings of the body rachis, radial and rare transverse on the pygidial pleurae; they are absent from the rachis and present as short fragments in the dorsal furrows. The panderian organs are asaphine.

**Comparison.** Similar to *A.?* *broeggeri* in the cephalon being elongated, in a weak relief of the carapace and, in particular, in the absence of the occipital furrow; however, it differs from the above species in the basal lobes being better expressed, in the absence of a ridgelike thickening at the posterior margin of the ocular area, and in the elongated pygidium. From *A. striatus*, it differs in shorter and lower eyes, in the presence of the lingula of the cranidium, an undivided pygidial rachis, and less developed terracelike folds. From the close species *A. acuminatus*, it differs in a wider and shorter lingula of the cranidium, in the absence of a

subdivision of the pygidial rachis, and in the absence of terracelike folds on it. The comparison with *A. lepidurus* is given under the description of the latter species. From *A. laevisimus*, it differs in the longer cephalon and pygidium, in the presence of rudiments of glabellar lobes, absence of the eye lists, in the marginal bend of the anterior branch of the facial suture being rounded, and in the pygidial rachis being undivided.

**Variability** is expressed in the presence of forms with a more convex carapace, a somewhat shortened cephalon and pygidium, more strongly developed furrows, including a preglabellar furrow and forms with a more flattened elongated carapace with weaker developed furrows and terracelike folds. The forms are usually rather large (Balashova, 1953, pl. 2, figs. 4, 5).

**Remarks.** A group of *Asaphus* which are very close to one another is present in the lower part of the Kunda Horizon; they consecutively replace each other in sections and apparently constitute a single phylogenetic line (Lamanskii, 1905, p. 62). They differ from each other in the size of their eyes, in the shape of the anterior end of the cranidium, and in the segmentation of the pygidial rachis. In the form occupying the lowermost position in sections (1), the eyes are very small, the cranidial lingula is narrow and long and the rachis is subdivided; in the form occupying the central position (2), the characters are the same, except for the larger eyes; and in the form occupying the upper position (3), the eyes are relatively large, the cranidial lingula is wide and short, and the rachis is undivided. Being rather difficult for identification, these forms have been repeatedly described under different names. It is impossible to determine which form is meant by this author on the basis of the short diagnosis provided; original specimens mentioned in earlier papers are almost lost. Judging from his figures, Angelin considered forms 1 and 2 belong to the species *A. raniceps* Dalman (Angelin, 1854, pl. 28, fig. 2). However, it is unclear, which of them may be associated with the variety *Asaphus expansus* var.  $\beta$ : *raniceps* that was established by Dalman (1828). Probably, it belongs to a completely separate species, which is not incorporated in the group under discussion (Nielsen, 1995, figs. 75a–75d). This entire group was identified by Schmidt (1901) as *A. raniceps* Dalman, with form 3 being typical and form 1 being the variety *A. raniceps* var. *lamanskii*. Jaanusson (1953a, p. 394) was the first to recognize the incompatibility of *A. raniceps* sensu Angelin–Schmidt with the original diagnosis and introduced the designation *A. "raniceps"*. His *A. "raniceps"* circulates widely in modern geological literature and has been included into the Regional Stratigraphical Chart of the Ordovician of the western part of the eastern European Platform as a leading form (*Resheniya...*, 1987), although its range is not restricted to the middle subhorizon but includes the entire lower subhorizon of the Kunda Horizon. *A. raniceps* s. str., i.e., form 3, has a longer history. It has appeared in Russian geological literature for nearly 100 years and also as a zonal species

(Lamanskii, 1905; Yanishevskii, 1932; Lesnikova and Weber, 1949; Balashova, 1953; Balashova and Balashov, 1959; Alikhova, 1960; Dmitrovskaya, 1989, 1991).

Hence, since Dalman's originals have not survived and the text and figures in his paper allow broad interpretation, and because the name *Asaphus raniceps* has a long tradition of use, it seems acceptable to keep it for designation of *Asaphus raniceps* forma typica sensu F. Schmidt. To avoid possible confusions, a specimen from Schmidt's collection has been selected as the neotype. Balashova's specimen (1953, pl. 2, fig. 4) belongs to the same form, but is not as well preserved and lacks some characters.

Forms 1 and 2 were also described under the name *A. acuminatus* Boeck. Regrettably, the form, which the lectotype of this species belongs to, cannot be identified due to its fragmentary preservation, only the pygidium is preserved more or less completely (Nielsen, 1995, fig. 68). Form 1 (*A. lamanskii*) received the status of zonal species after Lamanskii's research (Lamanskii, 1905; Balashova and Balashov, 1959; Alikhova, 1960). In the Ladoga Glint, it occurs in association with *A. expansus gracilis* and *A. expansus robustus*, whereas form 2 occurs with *A. expansus deltifrons*. As far as these forms are quite similar and have a close, but nevertheless different, stratigraphic distribution, I propose to treat them as subspecies of one species *A. acuminatus*, *A. acuminatus acuminatus* Boeck (form 2) and *A. acuminatus lamanskii* Schmidt (form 1).

**Occurrence.** Middle Ordovician, Llanvirn, Kunda Horizon, lower part of the *raniceps*-*striatus* Zone; Sillaoru Formation, Lopukhinka Member, Obukhovo Formation, Member 1. Outside the Ladoga Glint: Baltic Glint, Sillaoru Formation, Lopukhinka Member, lower part of the Loobu Formation; Estonia as a whole (Balashova, 1953, 1976; Rõõmusoks, 1960); Moscow Syncline, Valdai Monocline, Obukhovo Formation, central part, Veksino Formation (Dmitrovskaya, 1989, 1991); Jelgava Depression, Baldone Formation, Šupili and Ziemele members (Ulst *et al.*, 1984); southeastern Latvia (Gailite, 1978; Männil, 1963b, 1966); Latvian Saddle (Alikhova, 1960); northern slope of the Belorussian Massif, upper parts of the Pivory and Tvaracius formations (Lashkov *et al.*, 1983); Middle Lithuanian trough, Bičiunai Formation, Milkone and Obialis members, Rokiškis Formation, Juodupe Member (Lashkov *et al.*, 1984); northeastern Poland (Modlinski and Pokorski, 1964); Öland Island (Bonlin, 1949, 1955).

**Material.** One hundred and eighty-seven specimens: Lynna River, 0.1–0.5 m above ds3; Volkhov River, 0.15–0.8 m above ds3; quarry near the village of Vobokalo, 0.05–0.8 m above ds3; Lava River, 0.05–0.6 m above ds3; village of Putilovo, 0.05–0.3 m above ds3.

*Asaphus striatus* Boeck, 1838

Plate 4, figs. 6–8; Plate 5, figs. 1–3

*Asaphus striatus*: Sars, Boeck, 1838, p. 102 (cit. Brögger, 1882); Störmer, 1940, p. 141, pl. 3, figs. 12–15.

*Asaphus striatus*, forma typica: Brögger, 1882, p. 95, pl. 8, figs. 1–4.

*Asaphus pachyophthalmus*: Schmidt, 1901, p. 37 (part), figs. 26, 27.

*Asaphus eichwaldi* var. *lepiduroides*: Lamanskii, 1905, p. 63.

*Asaphus* (*Neosaphus*) *pachyophthalmus* var. *major*: Jaanusson, 1953a, p. 398.

*Asaphus* (*Trematophorus*) *pachyophthalmus*: Balashova, 1953, p. 397 (part).

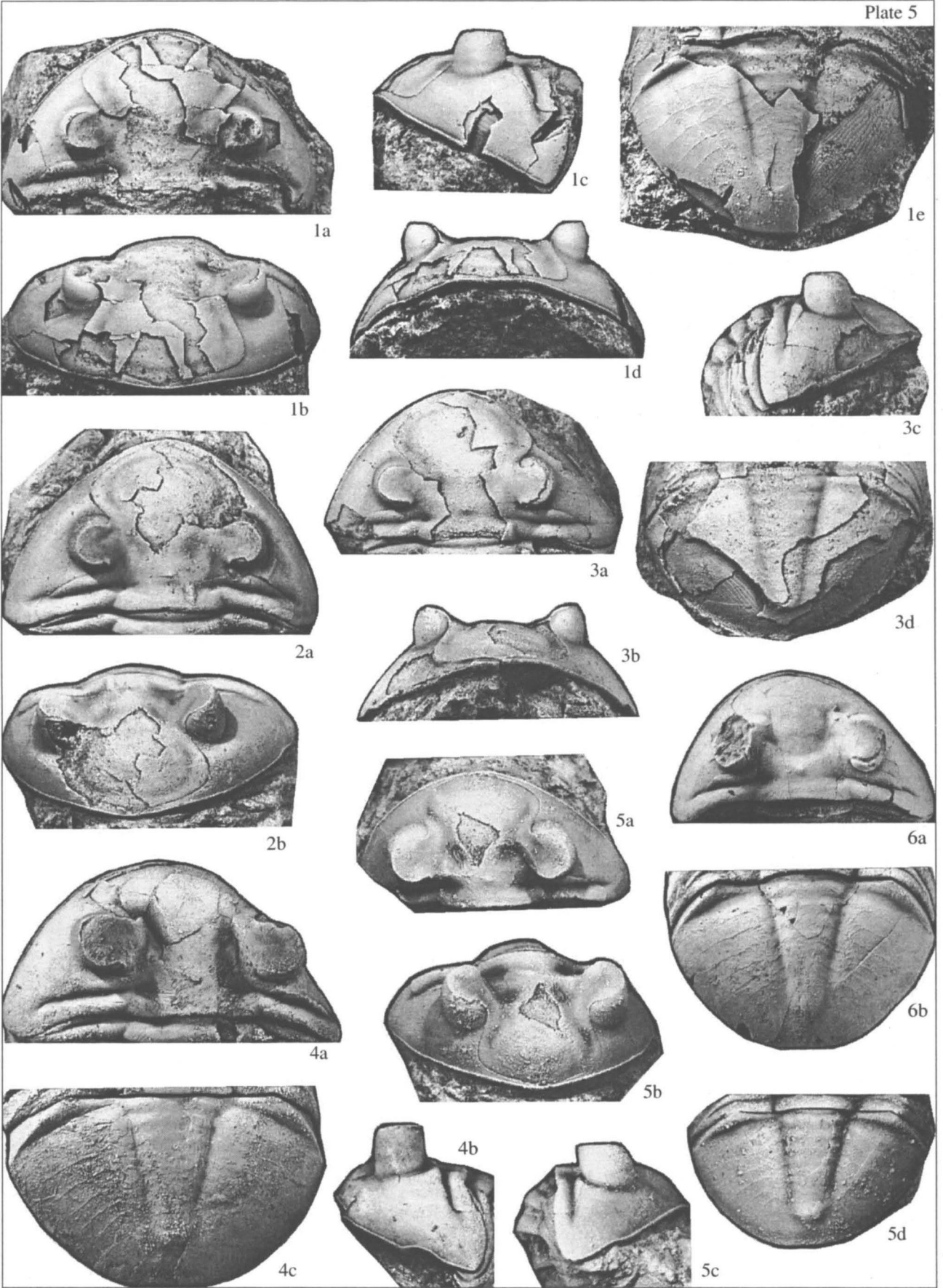
*Asaphus* (*Neosaphus*) *major*: Balashova, 1976, p. 12 (part).

*Asaphus* (*Asaphus*) *striatus*: Wandas, 1983, p. 218 (part), pl. 1, figs. H, I, and J, pl. 2, figs. A, F, H, and K; Nielsen, 1995, p. 91, figs. 70 and 71.

**H o l o t y p e** (monotype). PMO, no. 2634, cast of pygidial shield, depicted by Brögger (1882, pl. 8, fig. 4), designated and depicted by Wandas (1983, pl. 1, figs. H, I); Norway, Oslo Region, Eiker; *Orthoceras* Limestone.

**Diagnosis.** Cephalon elongated and medium-proportionate, with weak beaklike bend or without it; glabella not reaching far into the anterior margin; basal lobes lenslike; rudiments of glabellar lobes present; occipital furrow absent or represented by a pit; paradiabulral furrows absent; cranidium acuminate anteriorly; marginal bend of anterior branch of facial suture rounded; eyes medium-long and medium-high or high, removed from posterior margin at distance a little greater or a little less than their length; eye pedicles absent; eye lists absent; ocular areas not elevated above cephalon and barren of tubercles; occipital ring flat; pygidium medium-proportionate and elongated, with rounded lateral margins and posterior end; rachis faintly subdivided; terracelike folds absent from anterior part of frontal lobe and librigenae.

**Description.** The carapace is medium-sized and large, the maximum measured width of the cephalon is 54 mm. The cephalon is elongated and medium-proportionate (mean l/d, 0.5–0.56), acuminate anteriorly, with a weak beaklike bend or without it. The frontal lobe is weakly convex, with the maximum convexity in its middle part, not reaching far into the anterior margin, and weakly bordered anteriorly. The flexure between the frontal and medial lobes is weak. The medial lobe is weakly bordered laterally, the basal lobes are lenslike, weakly to sharply expressed, the rudiments of glabellar lobes are present, the frontal lobe bears a weak longitudinal ridge and a pit in front of it. The eyes are medium-long, medium-high and high, approximated to the posterior margin, being removed from it at a distance, which is a little greater or less than their length, and widely separated (mean lo/l, 0.25–0.31; mean ho/lo, 0.8–0.84; mean la/lp, 1.3–1.4; and mean do/d, 0.57–0.58), the eye socles are fully developed, the eye lists, eye ridge and a tubercle in the posterolateral corner of the ocular area are absent. The bends of the anterior branch of the facial suture are as following: the ocular one is absent, the marginal one is rounded, and the anterior one is almost not expressed. The cranidium is acuminate anteriorly. The distance



between the facial sutures at the level of marginal bends is greater than such a distance at the eye socles. The maximum width of the anterior part of the fixed gena is situated near the anterior margin of the shield. The dorsal furrows of the frontal lobe are shallow and medium-deep, those of the basal lobes are weakly expressed, the pseudodorsal furrows are shallow and unclear, the glabellar furrows are medium-deep, the fossulae are absent or rather distinct. The occipital furrow is absent or represented by a pit, the paradoublural furrow is absent. The occipital node is distinct. The librigenae are weakly convex to convex, the genal corners are somewhat obtuse to acuminate, the vincular pit is marked on the outer face by a bend in the lateral margin. The occipital ring is flat. Rings of the body rachis are flat to weakly convex. The pygidium is medium-proportionate or elongated (mean L/D, 0.58–0.64), with rounded lateral and posterior margins. The rachis is weakly segmented, with 2–4 segments which are visible on the carapace surface, faintly bordered from behind; the pleurae are flattened to weakly convex, smooth, lacking bordering behind the rachis. The following D-folds are present: weak or sharp on the rings of the body rachis, radial and transverse on the pygidial pleurae, and emphasizing segmentation and intercalary on its rachis. Individuals having terracelike folds alternating in height on the pygidial doublure occur occasionally (Pl. 5, fig. 3d). The panderian organs are hemiasaphine.

**Subspecies included.** *A. striatus striatus* Boeck, 1838 and *A. striatus sarsi* Brögger, 1882.

**Comparison with** *A. lepidurus*, *A. raniceps*, *A. acuminatus*, *A. knyrkoi*, *A. minutus*, *A. minor*, *A. pachyophthalmus*, *A. ingrianus*, *A. plautini*, and *A. ? broeggeri* is given under their descriptions.

**Remarks.** Redescribing this species, Wandas (1983) assigned it to *A. (Asaphus) Jaanusson* on the basis of a number of characters, including the asaphine panderian organs; he also mentioned eight or nine distinct segments on the pygidial rachis and treated forms with long and short pygidia as abnormal variabilities or deformations. The material on hand shows that the panderian organs of the first seven pleurae of the body are

represented by closed openings, which gradually shift to the margin of the doublure, reaching it, and transforming into a slotlike incisions on the last, eighth pleura. This type of the panderian organ is labeled here as hemiasaphine. As for the rachis segmentation, it follows from the published photograph that Wandas does not differentiate between the carapace and its cast, although the expression of the segmentation differs strikingly in the former and in the latter. Judging from the material on hand, it is clear that segments on the outer face of the rachial carapace are two to four, they are weak, whereas they are distinct and numerous in casts. As for forms with shortened and elongated pygidia, I incline to Brögger's opinion (Brögger, 1882) and recognize them as different subspecies, more so since their adult cephalons differ greatly. Their differences are more than subspecific, but the absence of well-preserved specimens of the same size prevent us from separating these forms into two independent species.

**Occurrence.** Middle Ordovician, Llanvirn, Kunda Horizon, upper part of the *raniceps-striatus* Zone; Obukhovo Formation, Members 3 and 4. Outside the Ladoga Glint: Baltic Glint (discovered specimens are ill-preserved and their identification is not completely reliable), Loobu Formation, upper part of the Utrias and lower part of the Valgejõe members; Norway, Oslo Region; *Orthoceras* Limestone, 3cγ (Störmer, 1940, 1953; Wandas, 1983), Huk Formation, 3cβ–3cγ according to labels of PMO.

*Asaphus striatus striatus* (Boeck, 1838)

Plate 5, figs. 1–3

*Asaphus striatus*: Sars, Boeck, 1838, p. 102 (cit. Brögger, 1882); Störmer, 1940, p. 141, pl. 3, figs. 12–15.

*Asaphus striatus*, forma typica: Brögger, 1882, p. 95, pl. 8, fig. 4.

*Asaphus pachyophthalmus*: Schmidt, 1901, p. 37 (part).

*Asaphus eichwaldi* var. *lepiduroides*: Lamanskii, 1905, p. 63.

*Asaphus (Trematophorus) pachyophthalmus*: Balashova, 1953, p. 397 (part).

*Asaphus (Neosaphus) major*: Balashova, 1976, p. 12 (part).

*Asaphus (Asaphus) striatus*: Wandas, 1983, p. 218 (part), pl. 1, figs. H, I, and J, pl. 2, figs. A, F, and H; Nielsen, 1995, p. 91, figs. 70 and 71.

Explanation of Plate 5

**Figs. 1–3.** *Asaphus striatus striatus* Boeck, 1838: (1) specimen PIN, no. 4330/32, bent, partially destroyed carapace,  $\times 1.5$ : (1a–1d) cephalon: (1a) dorsal view, (1b) view from the frontal lobe, (1c) side view, (1d) frontal view, (1e) pygidium; left bank of the Volkhov River, new bridge in the town of Volkhov; Kunda Horizon, Obukhovo Formation, Member 4, upper part of the *raniceps-striatus* Zone, talus; (2) specimen PIN, no. 4330/30, cephalon,  $\times 1.5$ : (2a) dorsal view, (2b) view from the frontal lobe; Putilovo outcrop; Kunda Horizon, Obukhovo Formation, Member 4, same age, 0.75 m below the formation roof; (3) specimen PIN, no. 4330/31, bent, partially destroyed carapace,  $\times 1.5$ : (3a–3c) cephalon: (3a) dorsal view, (3b) frontal view, (3c) side view, (3d) pygidium; right bank of the Volkhov River, Simankovo village; Kunda Horizon, Obukhovo Formation, Member 4, same age, 5.5 m above the floor of the formation, collected by Balashova.

**Figs. 4–6.** *Asaphus pachyophthalmus* F. Schmidt, 1901: (4) specimen PIN, no. 4330/36, unrolled, partially deformed carapace,  $\times 1.5$ : (4a, 4b) cephalon: (4a) dorsal view, (4b) side view, (4c) pygidium; Volkhov River, Volkhov hydroelectric power station dam outcrop; Kunda Horizon, Simankovo Formation, Member 1, upper part of the *minor-pachyophthalmus* Zone, 1.95 m below the 4 discontinuity surface; (5) specimen PIN, no. 4330/80, bent carapace of small individual,  $\times 2.5$ : (5a–5c) cephalon: (5a) dorsal view, (5b) view from the frontal lobe, (5c) side view, (5d) pygidium; Putilovo outcrop; Kunda Horizon, lower part of the Simankovo Formation, same age; (6) specimen PIN, no. 4330/35, unrolled carapace,  $\times 1.7$ : (6a) cephalon, (6b) pygidium; left bank of the Volkhov River, new bridge for motor traffic in the town of Volkhov; Kunda Horizon, Simankovo Formation, Member 1, same age, about 2 m above the floor of the member.

**Lectotype.** The type of the species

**Diagnosis.** Carapace medium-sized; cephalon and pygidium medium-proportionate; eyes medium-high, removed from posterior margin at a distance a little less than their length; fossulae absent; librigenae convex; genal corners acuminate; ring of body rachis and pygidial pleurae weakly convex.

**Comparison** with *A. striatus sarsi* is given under the description of the latter species.

**Remarks.** In the Lamanskii's collection (DPStPSU), several specimens of the variety *Asaphus eichwaldi* var. *lepiduroides* established by him survived. Their reexamination showed that it is a junior synonym of *A. striatus striatus*. Schmidt (1901) united several close forms with large eyes, including the species in question, in one species *A. pachyophthalmus*. However, the distribution of these forms differs and associates with certain stratigraphical levels, in addition to morphological differences, and they are good species.

**Occurrence.** Kunda Horizon, upper part of the *raniceps-striatus* Zone; Obukhovo Formation, Member 4. Outside the Ladoga Glint: Leningrad Region, Mishina Gora, stratigraphical position unknown; Norway, Oslo Region, Huk Formation, 3c $\beta$ - $\gamma$ .

**Material.** Twelve specimens: Volkhov River, Zvanka outcrop, 5.9 m above ds3; Putilovo outcrop, 4.0-4.1 m above ds3.

*Asaphus striatus sarsi* Brögger, 1882

Plate 4, figs. 6-8

*Asaphus striatus* var. *sarsi*: Brögger, 1882, p. 94, pl. 8, figs. 1-3.

*Asaphus pachyophthalmus* var. *major*: Schmidt, 1901, p. 41, figs. 26 and 27.

*Asaphus (Neasaphus) pachyophthalmus* var. *major*: Jaanusson, 1953a, p. 398.

*Asaphus (Neasaphus) major*: Balashova, 1976, p. 12 (part).

*Asaphus (Asaphus) striatus*: Wandas, 1983, p. 218 (part), pl. 2, fig. K.

**Lectotype.** PMO, no. 2616 carapace cast, depicted by Brögger (1882, pl. 8, fig. 2) and Wandas (1983, pl. 2, fig. K), designated here; Norway, Oslo Region; *Orthoceras* Limestone.

**Diagnosis.** Carapace large; cephalon and pygidium elongated; eyes high, removed from posterior margin at a distance a little greater than their length; eyes high, removed from posterior margin at a distance a little greater than their length; fossulae distinct; librigenae weakly convex; genal corners somewhat obtuse; rings of body rachis and pygidial pleurae flat.

**Comparison.** From *A. striatus striatus*, it differs in its mean size being much greater, in the elongated cephalon, higher eyes, which are removed farther from the posterior margin, in the fossulae being distinct, in having obtuse genal corners, less convex librigenae, more flat rings of the body rachis, and in a longer pygidium with more fattened pleurae.

**Remarks.** *Asaphus pachyophthalmus* var. *major* F. Schmidt (Schmidt, 1901, p. 40, text-figs. 26, 27), the only specimen of which is stored at GMAGI (no. 21/11152), refers to this subspecies. Balashova (1953) treated it as a separate species, *Asaphus (Schizophorus) major*, but, following Lamanskii, originally assigned an elongated form of *A. raniceps* to it as well (*ibid.*, pl. 2, fig. 5). In her last paper, Balashova (1976) refers both subspecies of *A. striatus* to *Asaphus (Neasaphus) major*, as follows from her description.

**Occurrence.** Kunda Horizon, upper part of the *raniceps-striatus* Zone; Obukhovo Formation, Member 3. Outside the Ladoga Glint: Baltic Glint, Loobu Formation, middle part; Norway, Oslo Region, 3c $\beta$ - $\gamma$ .

**Material.** Forty-two specimens: Lynna River, 5.7 m above ds3; Volkhov River, village of Simankovo, 5.5 m above ds3, Zvanka outcrop, 5-5.4 m above ds3 or 7.05-7.45 m below ds4; Lava River, 3.35-3.4 m above ds3; village of Putilovo, 2.8-3.3 m above ds3.

*Asaphus pachyophthalmus* F. Schmidt, 1901

Plate 5, figs. 4-6

*Asaphus pachyophthalmus*: Schmidt, 1898, p. 20 (nom. nud.); 1901, p. 37 (part), pl. 2, figs. 8-10, text-figs. 22-25; Lamanskii, 1905, p. 62; Lesnikova and Weber, 1949, p. 286, pl. 68, figs. 10 and 11.

*Asaphus (Trematophorus) pachyophthalmus*: Balashova, 1953 (part), p. 397, pl. 1, fig. 22 (?), 35 (?), pl. 2, figs. 10 and 11 (non pl. 4, fig. 21 = *S. laticaudatus*).

*Asaphus (Neasaphus) pachyophthalmus*: Jaanusson, 1953a, p. 398; Balashova, 1976, p. 14.

**Lectotype.** Specimen figured by Schmidt (1901, pl. 2, fig. 9), designated by Balashova (1953), specimen lost. Paralectotypes GMAGI, nos. 18/11152 and 19/11152.

**Diagnosis.** Cephalon middle-proportionate, with weak beaklike bend; glabella reaches anterior margin; basal lobes lenslike; rudiments of glabellar lobes present, occipital furrow shallow, developed along entire length or as a pit; paradoublural furrows absent; cranidium slightly obtuse anteriorly; marginal bend of anterior branch of facial suture rounded; eyes long, medium-high and high, removed from posterior end at a distance less than their length; eye pedicles absent; eye lists absent; ocular areas not elevated above cephalon and barren of tubercles; occipital ring flat; pygidium medium-proportionate, with rounded or straightened lateral margins and obtuse posterior end; rachis faintly subdivided; terracelike folds absent from anterior part of frontal lobe and librigenae.

**Description.** The carapace is medium-sized, the maximum measured width of the cephalon is 43 mm. The cephalon is medium-proportionate (mean l/d, 0.54), rounded anteriorly and has an anterior margin with a beaklike bend. The frontal lobe is moderately convex, with the maximum convexity in the middle, reaching the anterior margin, not bordered anteriorly, and lacking a longitudinal ridge. The medial lobe is weakly bordered laterally, the flexure between it and the frontal lobe is weak. The basal lobes are lenslike

and distinct. Rudiments of the glabellar lobes are present. The eyes are long, medium-high and high, approximated to the posterior end at the distance, which is somewhat less than their length, and widely separated (mean  $lo/l$  cp., 0.38; mean  $ho/lo$ , 0.82; mean  $la/lp$ , 1.4; and mean  $do/d$ , 0.61). The eye socles are fully developed. The ocular areas are not elevated above the cephalon. The eye pedicles, eye lists, and tubercles in the posterolateral corners of the ocular areas are absent. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded, and the anterior bend is absent. The cranidium is slightly obtuse anteriorly. The distance between the facial sutures at the level of the marginal bends is greater than such a distance at the eye socles. The anterior part of the fixed gena widens toward the anterior margin of the shield. The dorsal furrows are medium-deep and distinct in the frontal lobe and weakly expressed in the basal lobes. The pseudodorsal furrows are shallow and unclear. Glabellar furrows are medium-deep. The occipital furrow is shallow or developed along its entire length, or developed as a pit. The fossulae and paradoublural furrows are absent. The occipital node is distinct. The librigenae are weakly convex. The genal corners are acuminate. The vincular pits are expressed on the outer face as sharp bends in the shield margin. The occipital ring and rings of the body rachis are flat. The pygidium is medium-proportionate (mean  $L/D$ , 0.57), rounded in juvenile individuals and parallel-sided and a somewhat obtuse posterior end in adults, and flattened. The rachis is weakly segmented, with up to three segments visible on the carapace, sharply bordered posteriorly. The pleurae are flattened, smooth, lacking a bordering behind the rachis. Radial and transverse D-folds are present on the rings of the body rachis and pygidial pleurae. The panderian organs are neoasaphine.

**Variability.** Young individuals of this species have relatively larger eyes, which are closer approximated to the posterior end, flatter librigenae, less expressed vincular pits, and more rounded pygidium with rounded lateral margins.

**Comparison.** It differs from *A. sulevi* in the glabella reaching but not overhanging the anterior margin of the cephalon, in the eyes being longer and closer approximated to the posterior margin, the flattened occipital ring, the pygidium having straightened sides and weakly segmented rachis, and in the absence of terracelike folds from the frontal lobes and genae. Small specimens of this species are similar to small specimens of *A. latus* and large individuals of *A. minor*. From *A. latus*, *A. pachyophthalmus* differs in the absence of tubercles from the posterolateral corners of the ocular areas, paradoublural furrows and terracelike folds from the anterior margin of the cephalon; from *A. minor*, it differs in the relatively longer and higher eyes and in a longer pygidium. The comparison with *A. knyrkoi* is given under the description of the latter species. From *A. striatus*, it differs in the shorter cephalon and pygidium,

in the glabella reaching the anterior margin, in longer and higher eyes, in the obtuse cranidium, straight lateral margins and the posterior end of the pygidium.

**Remarks.** Schmidt (1901) noted variations in the development of vincular pits in this species, Balashova (1953) mentioned forms with the cephalon being elongated and somewhat acuminate anteriorly, less convex glabella, smaller eyes and with cephalon being shorter and rounded and having larger eyes. Apparently, these authors united *A. pachyophthalmus* and *A. striatus striatus*. An argument for the invalidity of the neotype designated by Balashova (1953) is given in the introductory part of Systematic Paleontology.

**Occurrence.** Middle Ordovician, Llanvirn, Kunda Horizon, upper part of the *minor-pachyophthalmus* Zone, Simankovo Formation, middle part of Member 1. Outside the Ladoga Glint: Baltic Glint, Popovka River, Krasnoe Selo town; Leningrad Region, station of Serebryanka, village of Samuilikovo upon Mishina Gora (Balashova, 1953, 1976); northeastern Poland (Modlinski and Pokorski, 1964).

**Material.** Twenty specimens: Volkhov River, Volkhov town, 1.85–3.85 m below ds4; Lava River, 8.25 m above ds3 or 2.25 m below ds4; village of Putilovo.

*Asaphus minutus* sp. nov.

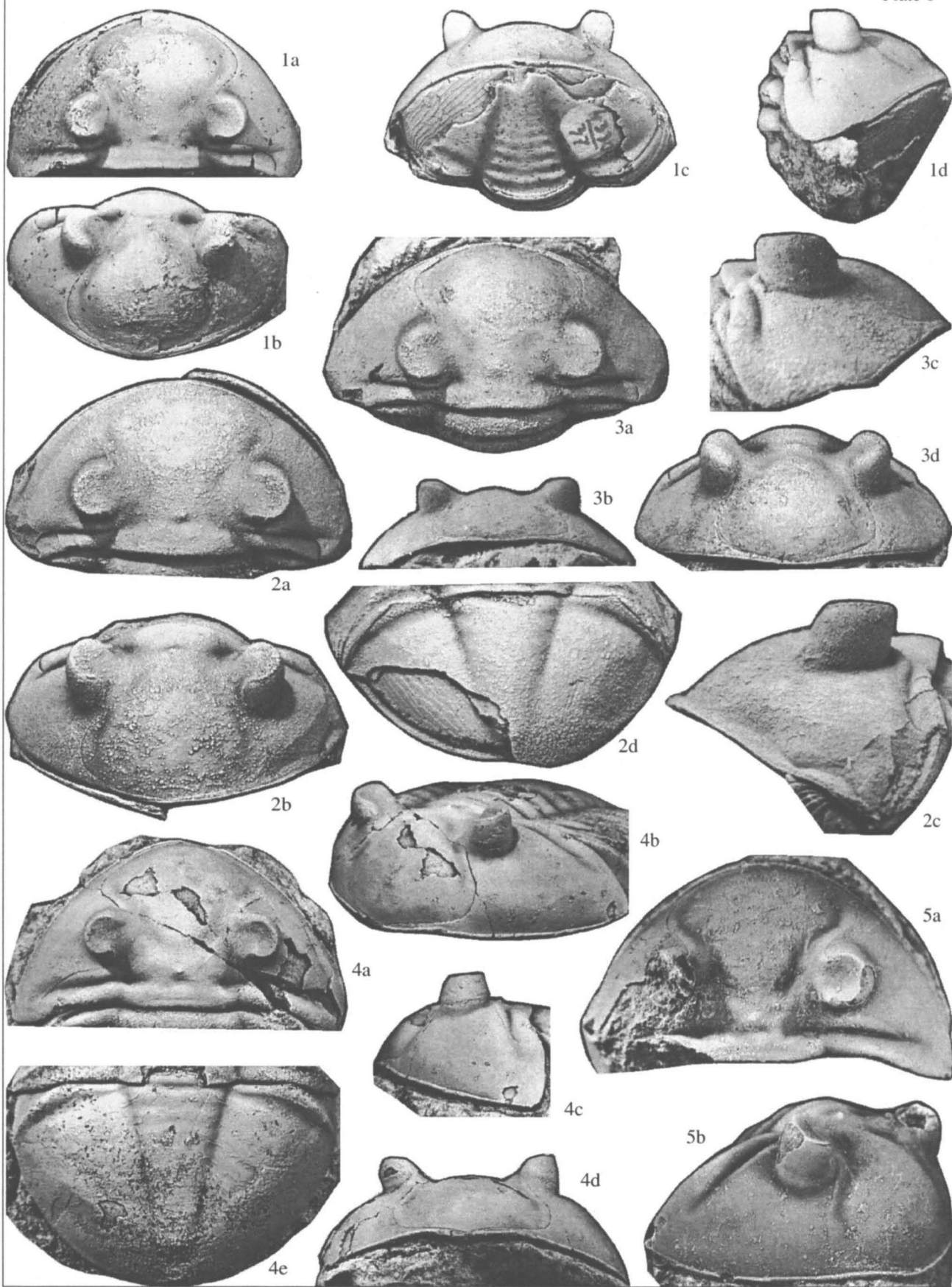
Plate 6, fig. 1

**Etymology.** From Latin *minutus* (minute).

**Holotype.** PIN, no. 4330/37, rolled, partially destroyed carapace; Lava River, Gorodishchenskii Kar'er outcrop (Fig. 5); 3.25 m above ds3; Middle Ordovician, Llanvirn, Kunda Horizon; middle part of the *raniceps-striatus* Zone (with *A. striatus sarsi*), Obukhovo Formation, upper part of Member 3 (Pl. 6, fig. 1).

**Diagnosis.** Cephalon medium-proportionate, without beaklike bend, glabella not reaching anterior margin; basal lobes lenslike; rudiments of glabellar lobes absent; occipital furrow shallow, developed along its entire length; paradoublural furrows absent; cranidium with small lingula anteriorly; marginal bend of anterior branch of facial suture rounded; eyes medium-long, high, removed from posterior end at a distance a little less than their length; eye pedicles absent; eye lists absent; ocular areas not elevated above cephalon and barren of tubercles; occipital ring flat; terracelike folds absent from anterior part of frontal lobe and librigenae.

**Description.** The carapace is small, the width of the cephalon of the holotype is 26.3 mm. The cephalon is medium-proportionate ( $l/d$ , 0.5), rounded anteriorly, without a beaklike bend in the anterior margin. The frontal lobe is convex, with the maximum convexity in the middle part, not reaching the anterior margin, bordered anteriorly with a weak furrow, and lacking a longitudinal ridge. The medial lobe is weakly bordered laterally, the flexure between it and the frontal lobe is



weak. The basal lobes are lenslike and almost not expressed. Rudiments of the glabellar lobes are absent. The eyes are medium-long, high, approximated to the posterior margin at a distance less than their length, and moderately separated ( $lo/l$ , 0.3;  $ho/lo$ , 0.85;  $la/lp$ , 2.2; and  $do/d$ , 0.55). The eye socles are fully developed. The ocular areas are not elevated above the cephalon. The eye pedicles, eye lists, and tubercles in the posterolateral corners of the ocular areas are absent. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded, and the anterior one is weak. The cranidium has a small lingula. The distance between the facial sutures at the level of the marginal bends is greater than such a distance at the eye socles. The anterior part of the fixed gena broadens toward the anterior margin of the shield. The dorsal furrows are weak on the frontal lobe and absent from the basal lobes; there are medium-deep diffused pseudodorsal furrows instead of them. Glabellar furrows are medium-deep. The occipital furrow is shallow, developed along its entire length. The fossulae and paradoublural furrows are absent. The occipital node is distinct. The librigenae are flat. The genal corners are somewhat obtuse. The vincular pits are marked by faint bends of the shield margin on the outer face. The occipital ring is flat. Rings of the body rachis are weakly convex. The structure of the pygidium has not been studied. D-folds are recorded on rings of the body rachis only. The structure of the pandeian organs is not known; they are possibly hemiasaphine.

**Comparison.** Similar to *A. minor* in the cephalon being shortened, approximated to the posterior margin eyes, and weak development of the furrows; however, it differs from *A. minor* in shorter but higher eyes, in the presence of a cranidial lingula, and in the occipital furrow being more strongly expressed.

**Remarks.** This species greatly resembles juvenile individuals of *A. striatus*, which is found in association with it, but differs in a shorter cephalon and smaller eyes, which are closer to the posterior margin of the cephalon.

**Occurrence.** Middle Ordovician, Llanvirn, Kunda Horizon, middle part of the *raniceps-striatus* Zone (with *A. striatus sarsi*); Obukhovo Formation, upper part of Member 3.

**Material.** Three carapaces: Volkhov River, village of Simankovo, 5.35 m above ds3; Lava River, 3.25 m above ds3.

### *Asaphus minor* F. Schmidt, 1901

Plate 6, figs. 2 and 3

*Asaphus pachyophthalmus* var. *minor*: Schmidt, 1901, p. 40, pl. 12, figs. 13 and 14.

*Asaphus (Trematophorus) minor*: Balashova, 1953, p. 398, pl. 2, fig. 6, pl. 4, fig. 7.

*Asaphus (Neoasaphus) pachyophthalmus* var. *minor*: Jaanusson, 1953a, p. 398.

*Asaphus (Neoasaphus) minor*: Balashova, 1976, p. 14.

**Lectotype.** GMAGI, no. 20/11152, deformed carapace, depicted by Schmidt (1901, pl. 12, fig. 14a), designated by Balashova (1953); Volkhov River, village of Zapolek; substage B<sub>3</sub>b.

**Diagnosis.** Cephalon medium-proportionate, without beaklike bend, glabella not reaching anterior margin; basal lobes lenslike; rudiments of glabellar lobes, occipital furrow, and paradoublural furrows absent; cranidium slightly obtuse anteriorly; marginal bend of anterior branch of facial suture rounded; eyes medium long and high, removed from posterior margin at a distance less than their length; eye pedicles and eye lists absent; ocular areas not elevated above cephalon and barren of tubercles; occipital ring flat; pygidium shortened, with rounded lateral margins and posterior end; rachis faintly subdivided; terracelike folds absent from anterior part of frontal lobe and librigenae.

**Description.** The carapace is medium-sized and small, the maximum measured width of the cephalon is 42 mm; mean d, 31 mm. The cephalon is medium-proportionate (mean  $l/d$ , 0.49), rounded anteriorly, without a beaklike bend in the anterior margin. The frontal lobe is weakly convex, with the maximum convexity in the posterior part, not reaching the anterior margin, not bordered anteriorly, and lacking a longitudinal ridge. The medial lobe is clearly bordered laterally, the flexure between it and the frontal lobe is absent. The basal lobes are lenslike, almost not expressed on the outer face of the carapace. Rudiments of the glabellar lobes are absent. The eyes are medium-long and medium-high, approximated to the posterior margin at a distance less than their length, widely separated (mean  $lo/l$ , 0.32; mean  $ho/lo$ , 0.77; mean  $la/lp$ , 2.2; and mean  $do/d$ , 0.57). The eye socles are fully developed. The ocular areas are not elevated above the cephalon. The eye pedicles, eye lists, and tubercles in

### Explanation of Plate 6

**Fig. 1.** *Asaphus minutus* sp. nov., holotype PIN, no. 4330/37, rolled, partially destroyed carapace,  $\times 2$ : (1a) dorsal view, (1b) view from the frontal lobe, (1c) frontal view, (1d) side view; Lava River, Gorodishchenskii Kar'er outcrop; Kunda Horizon, Obukhovo Formation, Member 3, middle part of the *raniceps-striatus* Zone (with *A. striatus sarsi*), 3.25 m above ds3.

**Figs. 2 and 3.** *Asaphus minor* F. Schmidt, 1901: (2) specimen PIN, no. 4330/39, rolled carapace: (2a–2c) cephalon: (2a) dorsal view,  $\times 2$ ; (2b) view from the frontal lobe,  $\times 2$ ; (2c) side view,  $\times 3$ ; and (2d) pygidium,  $\times 2$ ; Putilovo outcrop; Kunda Horizon, Obukhovo Formation, Member 4, lower part of the *minor-pachyophthalmus* Zone, 0.1 m below the roof of the formation; (3) specimen PIN, no. 4330/38, cephalon: (3a) dorsal view,  $\times 2$ ; (3b) frontal view,  $\times 1.5$ ; (3c) side view,  $\times 3$ ; and (3d) view from the frontal lobe,  $\times 2$ ; same age and locality, talus.

**Figs. 4 and 5.** *Asaphus knyrkoi* F. Schmidt, 1901: (4) specimen PIN, no. 4330/33, unrolled carapace,  $\times 1.5$ : (4a–4d) cephalon: (4a) dorsal view, (4b) half-turned view, (4c) side view, (4d) frontal view, (4e) pygidium; Volkhov River, Zvanka outcrop, 5.3 m above the floor of the Obukhovo Formation; (5) specimen PIN, no. 4330/181, cephalon,  $\times 2.5$ ; Putilovo outcrop, upper stage dump; Kunda Horizon, Obukhovo Formation, Member 4, upper part of the *raniceps-striatus* Zone (with *A. striatus striatus*).

the posterolateral corners of the ocular areas are absent. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded, the anterior one is absent. The cranidium is somewhat obtuse anteriorly. The distance between the facial sutures at the level of the marginal bends is greater than such a distance at the eye socles. The anterior part of the fixed gena widens toward the anterior margin of the shield. The dorsal furrows are small and weakly expressed on the frontal lobe and absent from the basal lobes. The pseudodorsal furrows are shallow and unclear. The glabellar furrows are shallow. The occipital furrow is shallow, developed along its entire length. The fossulae and paradoublural furrows are absent. The occipital node is distinct. The librigenae are flat. The genal corners are somewhat obtuse. The vincular pits are not expressed on the outer face. The occipital ring is flat. Rings of the body rachis are convex. The pygidium is shortened (mean L/D, 0.51), with rounded lateral and posterior margins. The rachis is weakly segmented, with up to three segments visible on its carapace, weakly bordered from behind. The pleurae are weakly convex, smooth, lacking bordering behind the rachis. Radial D-folds are present on rings of the body rachis and pygidial pleurae. The panderian organs are neosaphine.

**Comparison.** From *A. striatus*, it differs in a shorter cephalon, the glabella being unclear bordered anteriorly, the eyes situated closer to the posterior margin of the shield, and in a shorter pygidium. The comparison with *A. minutus* and *A. pachyophthalmus* is given under their description.

**Remarks.** Arguing for invalidity of the neotype designated by Balashova (1953) is given in the introductory part of Systematic Paleontology.

**Occurrence.** Middle Ordovician, Llanvirn, Kunda Horizon, lower part of the *minor-pachyophthalmus* Zone; Obukhovo Formation, upper part of Member 4; Sinyavino Formation; Simankovo Formation, lower part of Member 1. Outside the Ladoga Glint: Baltic Glint, Napa Formation (Rõõmusoks, 1960; Balashova, 1976); village of Sillamägi (specimens TMN, no. 96/62); Leningrad Region, Mishina Gora; central part of the Moscow Syncline (Alikhova, 1960).

**Material.** Forty-four specimens: Volkhov River, Volkhov town, 4.6–4.95 m below ds4, village of Zvanka, 7.35–7.8 m above ds3 or 4.6–5.1 m below ds4, village of Plekhanovo, 8.05 m above ds3 or 4.65 m below ds4; Lava River, 5.5–6 m above ds3 or 4.5–5 m below ds4; village of Putilovo, 4–5.2 m above ds3.

*Asaphus knyrkoi* F. Schmidt, 1901

Plate 6, figs. 4 and 5; Plate 12, figs. 5 and 6; Plate 21, fig. 4

*Asaphus eichwaldi* var. *knyrkoi*: Schmidt, 1901, p. 41, figs. 29–32.

*Asaphus eichwaldi* var. *expansoides*: Lamanskii, 1905, p. 63.

*Asaphus (Neosaphus) eichwaldi* var. *knyrkoi*: Jaanusson, 1953a, p. 398.

*Asaphus (Trematophorus) knyrkoi*: Balashova, 1953, p. 401, pl. 1, fig. 27 (?), pl. 5, fig. 8 (?) (non pl. 5, figs. 6, 7 = *A. sulevi*).

*Asaphus (Multiasaphus) knyrkoi*: Balashova, 1976, p. 9.

**Lectotype.** Specimen depicted by Schmidt (1901, fig. 32) and designated by Balashova (1953), was lost. Paralectotypes DHGStPSU, no. 149 (Schmidt, 1901, fig. 30), GMAGI, no. 30/11152 (specimen from Schmidt's collection, which was not figured); Volkhov River, village of Zapolek; substages B<sub>3</sub>b–C<sub>1</sub>a.

**Diagnosis.** Cephalon medium-proportionate, with a weak beaklike bend; glabella reaches anterior margin; basal lobes lenslike; rudiments of glabellar lobes absent; occipital furrow shallow, developed along its entire length; paradoublural furrows present; cranidium slightly obtuse anteriorly; marginal bend of anterior branch of facial suture rounded; eyes medium long and high; removed from posterior margin at distance approximately equal to their length; eye pedicles and eye lists absent; ocular areas not elevated above cephalon and barren of tubercles; occipital ring flat; pygidium elongated, with rounded lateral margins and somewhat obtuse posterior end; rachis low, weakly segmented; terracelike folds present on anterior part of frontal lobe and absent from librigenae, alternating in height on pygidial doublure; dorsal face of carapace coarsely pitted.

**Description.** The carapace is medium-sized and large, the maximum measured width of the cephalon is 48 mm; mean d, 45 mm. The cephalon is medium-proportionate (mean l/d, 0.48), weakly acuminate anteriorly, having a weak beaklike bend. The frontal lobe of the glabella is strongly convex, with the maximum convexity in the anterior or middle part, reaching the anterior margin, bordered with a weak furrow anteriorly, lacking a longitudinal ridge. The medial lobe is weakly bordered laterally, the flexure between it and the frontal lobe is absent. The basal lobes are lenslike. Rudiments of the glabellar lobes are absent. The eyes are medium-long and medium-high, shifted to the posterior margin of the shield at a distance, which is nearly equal to their length, approximated (mean lo/l, 0.32; mean ho/lo, 0.77; mean la/lp, 1.5; and mean do/d, 0.52). The eye socles are fully developed. The eye pedicles, eye lists, and tubercle in the posterolateral corners of the ocular areas are absent. The ocular areas are not elevated above the cephalon. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded, the anterior one is absent. The cranidium is somewhat obtuse anteriorly. The distance between the facial sutures at the marginal bends is greater than such a distance at the eye socles. The maximum width of the anterior part of the fixed gena is at the fossula. The dorsal furrows are medium-deep on the frontal lobe and absent from the basal lobes. The glabellar furrows are absent. The pseudodorsal furrows are absent. The occipital furrow is shallow, developed along its entire length. The fossulae are unclear. The paradoublural furrows are present. The occipital node is distinct. The librigenae are con-

vex. The genal corners are acuminate. The vincular pits are not expressed on the outer face. The occipital ring and rings of the body rachis are flat. The pygidium is elongated (mean L/D, 0.62), with rounded lateral margins and a slightly obtuse posterior end. The anterior part of the rachis is low and seems to be depressed into the shield surface, the rachis is weakly segmented, with up to three segments visible on the carapace surface, and weakly bordered posteriorly. The pleurae are convex, smooth, and lack bordering behind the rachis. The pygidial doublure is broad, with a peculiar regular alternation of high and low terracelike folds ("thick and thin terrace lines" in Balashova's descriptions (1953, 1976)) (Pl. 12, fig. 5). The following D-folds are present: emphasizing segmentation and intercalary folds on the entire surface of the glabella (very thin), occipital ring and rings of the body rachis, and on the pygidial rachis and radial and transverse folds on the pygidial pleurae. The sculpture is represented by rather large and dense pits, which cover the entire surface of the carapace (Pl. 12, fig. 6). These pits are larger than usual for *Asaphus* pore openings (Balashova, 1955) but smaller than "sensorial bristle pores" that are present on the librigenae of some species. The panderian organs are neosaphine.

**C o m p a r i s o n.** This species differs from all other species in the peculiar sculpture of its carapace. From *A. expansus*, it differs in somewhat longer eyes, lenslike basal lobes, the presence of paradoublural furrows, a weaker occipital furrow, the flat occipital ring, and in the elongated pygidium possessing weakly segmented rachis; from *A. pachyophthalmus*, it differs in many characters, including smaller eyes and the presence of the paradoublural furrows; from *A. ingrianus*, it differs in the rounded marginal bend of the anterior branch of the facial suture, shallower furrows on the cephalon, the presence of paradoublural furrows, the flat occipital ring, and in the elongated pygidium possessing a weaker segmented rachis. The comparison with *A. sulevi* is given under the description of the latter species. It is similar to the species *A. striatus* (subspecies *A. striatus striatus*), which is found in association, in the rather large eyes being approximated to the posterior margin, in the furrows being equally developed, in the peculiar alternation of the terracelike folds on the pygidial doublure; however, it differs in the cranidium being somewhat obtuse, the absence of rudiments of the glabellar lobes, the presence of paradoublural furrows, and the pygidium obtuse from behind, in addition to the distinctive sculpture on the dorsal face of the carapace.

**R e m a r k s.** An argument for the invalidity of the neotype designated by Balashova (1953) is given in the introductory part of Systematic Paleontology.

**O c c u r r e n c e.** Ladoga Glint; Middle Ordovician, Llanvirn, middle part of the Kunda Horizon, upper part of the *raniceps-striatus* Zone – lower part of the *minor-pachyophthalmus* Zone; Obukhovo Formation, Member 4.

**M a t e r i a l.** Seventy-seven specimens: Volkhov River, village of Zvanka, 5.4–6.1 m above ds3 or 6.35–7.05 m below ds4, Plekhanovo River, 5.55–5.65 m above ds3 or 7.05–7.15 m below ds4; Lava River, 4.05–4.15 m above ds3 or 5.35–5.45 m below ds4; village of Putilovo, 3.65–4.05 m above ds3.

*Asaphus sulevi* Jaanusson, 1953

Plate 7, figs. 1–4

*Asaphus eichwaldi*: Schmidt, 1898, p. 22 (nom. nud.); 1901, p. 41, pl. 4, figs. 6, 9, and 10, text-figs. 7, 28a, and 28b (?) (non pl. 12, figs. 20, 21 = *A. ingrianus* Jaanusson); Lesnikova and Weber, 1949, p. 286, pl. 68, fig. 13 (non pl. 68, fig. 12 = *A. ingrianus*); non *Asaphus eichwaldi* Fischer, 1825.

*Asaphus (Trematophorus) eichwaldi*: Balashova, 1953, p. 399, pl. 1, fig. 25 (?) (non pl. 2, figs. 12, 13 = *A. ingrianus*).

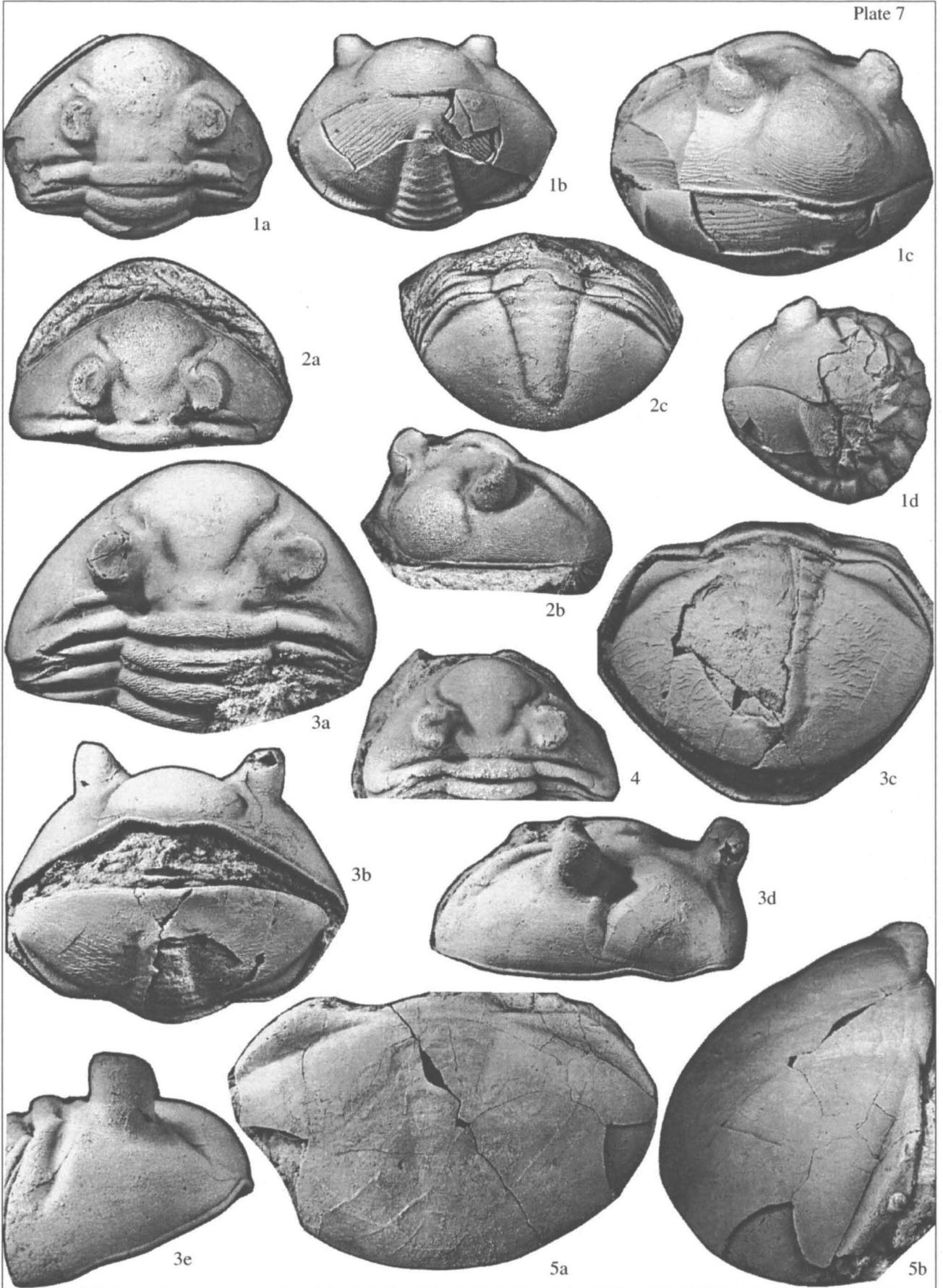
*Asaphus (Neoasaphus) sulevi*: Jaanusson, 1953a, p. 393.

*Asaphus (Neoasaphus) eichwaldi*: Balashova, 1976, p. 15.

**N e o t y p e.** GMAGI, no. 26/11152, carapace, depicted by Schmidt (1901, pl. 4, fig. 10), designated here; Pavlovsk town; substages B<sub>3</sub>b–C<sub>1</sub>a.

**D i a g n o s i s.** Cephalon medium-proportionate, with weak or abrupt beaklike bend; glabella reaching anterior margin and overhanging it; basal lobes lenslike; rudiments of glabellar lobes absent; occipital furrow shallow or deep, developed along its entire length; paradoublural furrows absent; cranidium slightly obtuse anteriorly; marginal bend of anterior branch of facial suture rounded; eyes medium-long, high, removed from posterior end at distance approximately equal to their length; eye pedicles and eye lists absent; ocular areas not elevated above cephalon and barren of tubercles; occipital ring convex to flat; pygidium medium-proportionate, with rounded lateral margins and posterior end; rachis coarsely segmented; terracelike folds on anterior part of frontal lobe and on librigenae present.

**D e s c r i p t i o n.** The carapace is medium-sized and occasionally large, the maximum measured width of the cephalon is 55.4 mm; mean d, 35 mm. The cephalon is medium-proportionate (mean l/d, 0.49), rounded or weakly acuminate anteriorly, having a weak or abrupt beaklike bend. The frontal lobe of the glabella is strongly convex, with the maximum convexity in the anterior part, reaching the anterior margin and overhanging it, bordered with a weak or sharp furrow anteriorly, and lacking a longitudinal ridge. The medial lobe is weakly or sharply bordered laterally, the flexure between it and the frontal lobe is weak or sharp. The basal lobes are lenslike and weakly separated. Rudiments of the glabellar lobes are absent. The eyes are medium-long, medium-high or high, approximated to the posterior margin of the shield at a distance approximately equal to or somewhat less than their length, and moderately separated (mean lo/l, 0.3; mean ho/lo, 0.85; mean la/lp, 1.6; and mean do/d, 0.54). The eye socles are fully developed. The eye pedicles are absent or just outlined. The ocular areas are not elevated above the



cephalon. The eye lists and tubercles in the posterolateral corners of the ocular areas are absent. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded, the anterior one is absent. The cranidium is somewhat obtuse anteriorly. The distance between the facial sutures at the level of the marginal bends is greater than such a distance at the eye socles. The anterior part of the librigena is parallel-sided. The dorsal furrows are deep on the frontal lobe and shallow on the basal lobes. The glabellar furrows are medium-deep or deep, fused with medium-deep pseudodorsal furrows. The occipital furrow is shallow or deep, developed along its entire length. The fossulae and paradoublural furrows are absent. The occipital node is diffused. The librigenae are convex. The genal corners are somewhat obtuse. The vincular pits are not expressed on the outer surface or marked by weak bends in the lateral margin. The occipital ring is flat or convex. Rings of the body rachis are convex. The pygidium is medium-proportionate (mean L/D, 0.58), with rounded or slightly straightened lateral margins and a rounded posterior end. The rachis is coarsely segmented (up to 5 segments are visible), abruptly bordered from behind. The pleurae are flattened to convex, smooth, lacking a bordering posterior of the rachis. The D-folds are rough, developed over the entire surface of the glabella, librigenae, anterior parts of the fixed genae, occipital ring and rings of the body rachis; they emphasize segmentation on the pygidial rachis; and on the pygidial pleurae, they are radial and transverse. The panderian organs are neosaphine.

**Variability.** This species is highly variable. There are two forms at least, one of them (Pl. 7, figs. 1, 2) differs from the other in a more convex frontal lobe of the glabella, a more weakly expressed beaklike bend, less sharp flexure between the frontal and medial lobes, shallower glabellar and occipital furrows, low eyes, a less convex occipital ring and rings of the body rachis, and coarser terracelike folds on the anterior part of the glabella and on the librigenae. The above differences are enough for separation of a new species; however, the material on hand does not allow recognition of a difference in the stratigraphic and geographic distribution of forms, and at the same time, nearly continuous rows

may be recognized for the degree of expression of these characters.

**Comparison.** This species is closest to *A. ingrianus*, from which it differs in the glabella reaching the anterior margin and overhanging it, a deeper occipital furrow, rounded marginal bend of the anterior branch of the facial suture, and in the presence of terracelike folds on the genae. It is similar to *A. expansus*, *A. pachyophthalmus*, *A. kotlukovi*, and *A. knyrkoi* in the general shape of the cephalon. The comparison with the first two species is given under their description. From *A. kotlukovi*, it differs in lower eyes, the eye pedicles and tubercles in the posterolateral corners of the ocular areas being absent, and in the presence of terracelike folds on the genae. From *A. knyrkoi*, it differs in the glabella overhanging the anterior margin of the frontal lobe, deeper furrows on the cephalon, convex occipital ring, a shorter pygidium possessing coarser segmented rachis, presence of terracelike folds on the genae, and in the absence of (a characteristic of *A. knyrkoi*) a carapace sculpture and a terracelike folds on the pygidial doublure alternating in height.

**Remarks.** Balashova (1976) questioned the correctness of treating *Asaphus eichwaldi* F. Schmidt, 1901 as an objective homonym of *Asaphus eichwaldi* Fischer, 1825; however, Jaanusson's action (1953a) agrees well with the International Code of Zoological Nomenclature.

The specimen of *A. eichwaldi* from Schmidt's paper selected as the holotype of *Asaphus (Neosaphus) sulevi* by Jaanusson is lost. Some specimens cannot be identified correctly without comparing with the type. Hence, the neotype is designated here.

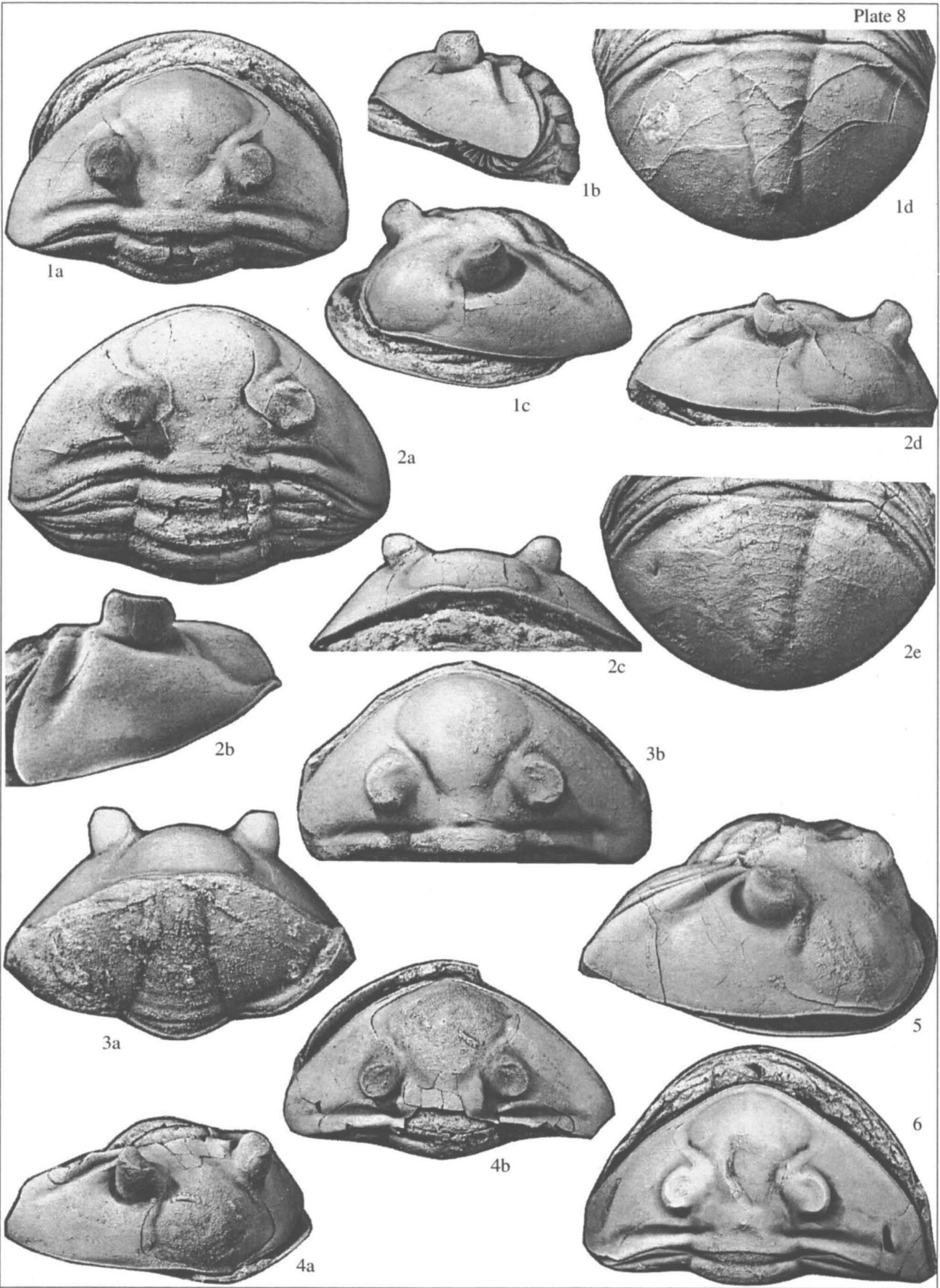
There is a specimen possibly belonging to this species and coming from the Oslo Region (3c, *Orthoceras* Limestone) in the collection of the Paleontological Museum, Oslo University (PMO, no. 1819).

**Occurrence.** Middle Ordovician, Llanvirn, Kunda Horizon, lower part of the *sulevi-ingrianus* Zone; Simankovo Formation, upper part of Member 1. Outside the Ladoga Glint: Baltic Glint, upper parts of the Sinyavino, Loobu, and Napa formations; Norway, Oslo Graben, 3c. On the basis of bibliographic data, this species (sensu Jaanusson, i.e., including *A. ingrianus*), and forms identified as *A. cf. sulevi* are distrib-

#### Explanation of Plate 7

**Figs. 1–4.** *Asaphus sulevi* Jaanusson, 1953: (1) specimen PIN, no. 4330/42, rolled, partially destroyed carapace: (1a) dorsal view,  $\times 1.5$ ; (1b) frontal view,  $\times 1.5$ ; (1c) half-turned view,  $\times 2$ ; and (1d) side view,  $\times 1.5$ ; Putilovo outcrop; Simankovo Formation, lower part of the *sulevi-ingrianus* Zone, talus; (2) specimen PIN, no. 4330/83, rolled carapace,  $\times 2$ : (2a, 2b) cephalon: (2a) dorsal view, (2b) half-turned view. (2c) pygidium; same age and locality, talus; (3) specimen PIN, no. 4330/46, rolled, partially destroyed carapace: (3a–3c) general appearance: (3a) dorsal view, (3b) frontal view, (3c) ventral view,  $\times 1.5$ ; (3d, 3e) cephalon: (3d) half-turned view,  $\times 1.5$ ; (3e) lateral view,  $\times 2$ ; left bank of the Volkhov River, new bridge for motor traffic in the town of Volkhov; Kunda Horizon, Simankovo Formation, Member 1, same age, 1.1 m below ds4; (4) specimen PIN, no. 4330/169, cephalon,  $\times 2$ ; Volkhov River, Zvanka outcrop; Simankovo Formation, Member 1, same age, talus.

**Fig. 5.** *Asaphinae?* gen. et sp. indet., specimen PIN, no. 4330/140, pygidium,  $\times 1$ : (5a) dorsal view, (5b) view from the right facet; right bank of the Lava River at the northern outskirts of the village of Naziya; Aseri Horizon, Duboviki Formation, beds with *A. intermedius*–*A. kowalewskii*.



uted on the Baltic Glint, Napa Formation (Balashova, 1953, 1976; Rõõmusoks, 1960), in northeastern Poland (Modlinski, 1973), and on Öland Island (Bohlin, 1955).

**Material.** One hundred and forty-nine specimens: Volkhov River, 0.45–1.4 m below ds4; Lava River, 1.25–2 m below ds4; village of Putilovo, 1.75–2.7 m above the floor of the Sinyavino Formation.

*Asaphus ingrianus* Jaanusson, 1953

Plate 8, figs. 1–4

*Asaphus eichwaldi* var. *applanata*: Schmidt, 1901, p. 44, pl. 4, fig. 11.

*Asaphus eichwaldi*: Schmidt, 1901, pl. 12, figs. 20, 21; Lesnikova and Weber, 1949, pl. 68, fig. 12.

*Asaphus (Neosaphus) sulevi ingrianus*: Jaanusson, 1953a, p. 393.

*Asaphus (Trematophorus) applanatus*: Balashova, 1953, p. 402, pl. 1, fig. 11 (?), 38 (?), pl. 4, fig. 20, pl. 5, fig. 5.

*Asaphus (Trematophorus) eichwaldi*: Balashova, 1953, p. 399, pl. 2, figs. 12 and 13.

*Asaphus (Neosaphus) ingrianus*: Balashova, 1976, p. 16.

**Holotype.** GMAGI, no. 31/11152, rolled and partially destroyed carapace, depicted by Schmidt (1901, pl. 4, fig. 11), designated by Jaanusson (1953a); Lava River, village of Vasil'kovo; substages B<sub>3</sub>b–C<sub>1</sub>a.

**Diagnosis.** Cephalon medium-proportionate, with sharp beaklike bend; glabella not reaching small anterior margin; basal lobes lenslike; rudiments of glabellar lobes absent; occipital furrow shallow, developed along its entire length; paradoublural furrows absent; cranidium acuminate anteriorly; marginal bend of anterior branch of facial suture sharp angular; eyes medium-long, high, removed from posterior margin for approximately their length; eye pedicles and eye lists absent; ocular areas not elevated above cephalon and barren of tubercles; occipital ring convex; pygidium medium-proportionate, with rounded lateral margins and posterior end, rachis coarsely segmented; terrace-like folds present on anterior part of frontal lobe and on occipital ring and absent from librigenae.

**Description.** The carapace is medium-sized, sometimes large, the maximum measured width of the cephalon is 57 mm; mean d, 36.5 mm. The cephalon is medium-proportionate (mean l/d, 0.48), anteriorly acuminate, with a sharp beaklike bend. The frontal lobe

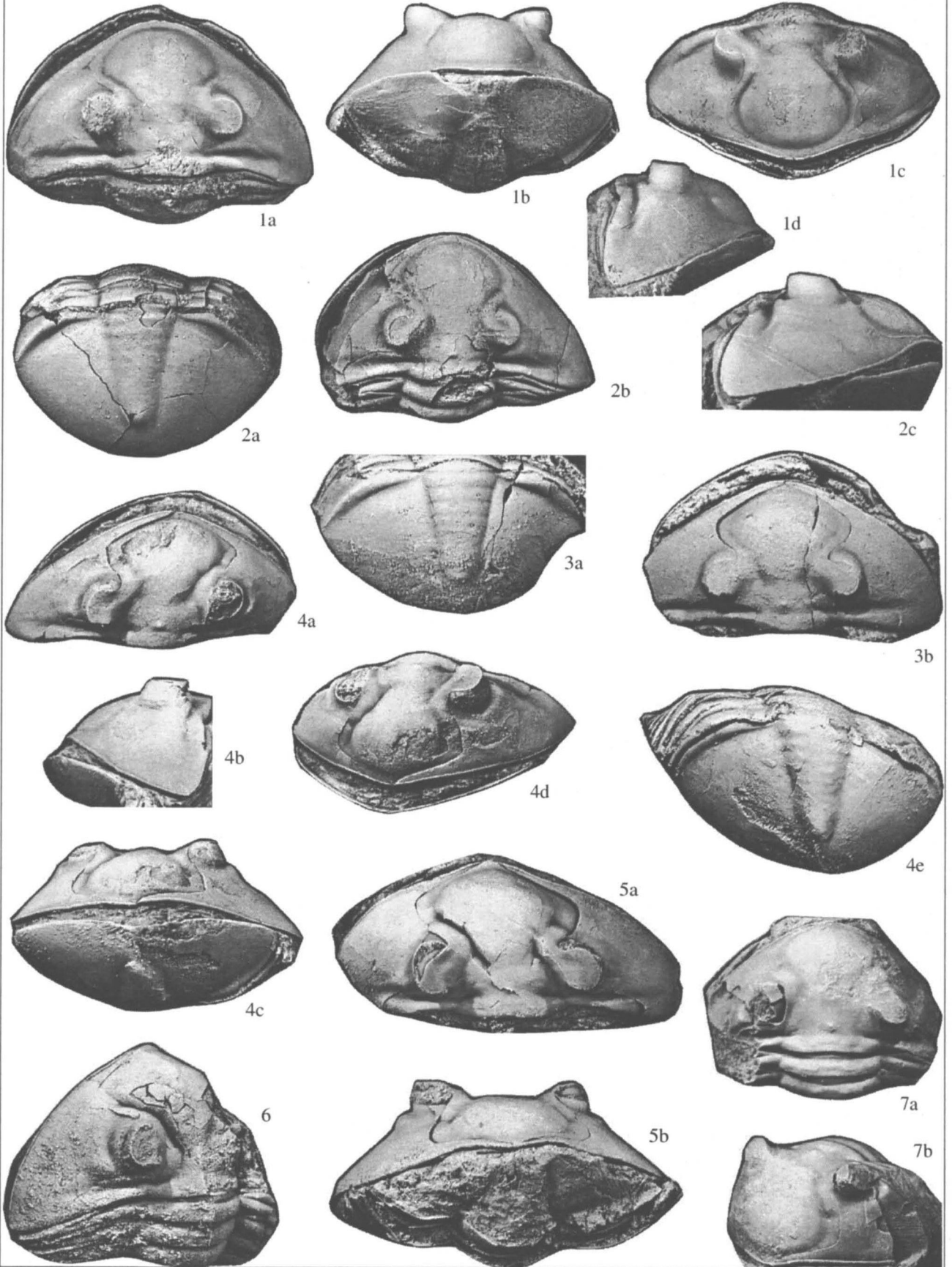
of the glabella is medium and strongly convex, with the maximum convexity on the anterior or middle part, not reaching the anterior margin, anteriorly bordered with a sharp furrow, and bears a longitudinal ridge. The medial lobe is abruptly bordered laterally, the flexure between it and the frontal lobe is sharp. The basal lobes are lenslike. Rudiments of the glabellar lobes are absent. The eyes are medium-long, high, shifted to the posterior margin of the shield for the distance close to their length, approximated (mean lo/l, 0.28; mean ho/lo, 0.86; mean la/lp, 1.9; and mean do/d, 0.5). The eye socles are fully developed. The eye pedicles, eye lists, and tubercle in the posterolateral corners of the ocular areas are absent. The ocular areas are not elevated above the cephalon. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is sharp and angular, and the anterior one is faintly visible. The cranidium is acuminate anteriorly. The distance between the facial sutures at the level of the marginal bends is greater than such a distance at the eye socles. The maximum width of the anterior part of the fixed gena is situated near the anterior margin of the shield. The dorsal furrows are sharp and deep on the frontal lobe and small, weakly expressed or distinct on the basal lobes. The glabellar furrows are deep, fused with the medium-deep pseudo-dorsal furrows. The occipital furrow is shallow, developed along its entire length. The fossulae and paradoublural furrows are absent. The occipital node is distinct. The librigenae are flat. The genal corners are somewhat obtuse. The vincular pits are not expressed on the outer face. The occipital ring and rings of the body rachis are convex. The pygidium is medium-proportionate (mean L/D, 0.57), with rounded lateral and posterior margins. The rachis is coarsely segmented (seven or eight segments are visible), abruptly bordered from behind. The pleurae are flattened, smooth, and lack a bordering posteriad of the rachis. Emphasizing segmentation D-folds are present on the anterior part of the frontal lobe of the glabella, occipital ring, rings of the body rachis, and on the pygidial rachis. The panderian organs are neosaphine.

**Variability.** Little variability is recorded in the following characters: the sharpness of the cephalon, the development of a beaklike bend, the convexity of the

Explanation of Plate 8

**Figs. 1–4.** *Asaphus ingrianus* Jaanusson, 1953: (1) specimen PIN, no. 4330/45, rolled carapace,  $\times 1.5$ : (1a–1c) cephalon: (1a) dorsal view, (1b) side view, (1c) half-turned view, (1d) pygidium; Putilovo outcrop; Simankovo Formation, Member 1, upper part of the *sulevi-ingrianus* Zone, talus; (2) specimen PIN, no. 4330/82, rolled carapace: (2a–2c) cephalon: (2a) dorsal view,  $\times 1.5$ ; (2b) side view,  $\times 2$ ; (2c) frontal view,  $\times 1.5$ ; (2d) half-turned view,  $\times 1.5$ ; (2e) pygidium; left bank of the Volkhov River, village of Plekhanovo; same stratigraphical position and age, talus; (3) specimen PIN, no. 4330/81, rolled carapace,  $\times 2$ : (3a) frontal view, (3b) dorsal view; Volkhov River, Volkhov hydroelectric power station dam outcrop, same stratigraphical position and age, 0.55 m below ds4; (4) specimen PIN, no. 4330/43, rolled, partially destroyed carapace,  $\times 1.5$ : (4a) half-turned view, (4b) dorsal view; Ruditsa River near the village of Lopukhinka; Kunda Horizon, Sinyavino Formation, same age, talus.

**Figs. 5 and 6.** *Asaphus laevissimus* F. Schmidt, 1901: (5) specimen PIN, no. 4330/86, rolled carapace of large individual,  $\times 1.5$ ; left bank of the Lava River, 100 m downstream of the Kavra River mouth; Kunda Horizon, Simankovo Formation, Member 2, *laevissimus* Zone; (6) specimen PIN, no. 4330/122, rolled carapace of large individual,  $\times 1.5$ ; Volkhov River, Volkhov hydroelectric power station dam outcrop; Kunda Horizon, Simankovo Formation, Member 2, same age, talus.



frontal lobe of the glabella, the relative length of the eyes, their approximation and shift to the posterior margin.

**Comparison** with *A. sulevi* and *A. knyrkoi*, which were united with the species under description in *Asaphus eichwaldi* (Schmidt, 1901; Lamanskii, 1905), and with *A. lepidurus*, *A. kotlukovi*, and *A. bottnicus* is given under their descriptions. It is similar to *A. laevis-simus* and *A. heckeri* in the sharp angular marginal bend of the anterior branch of the facial suture and in the weak development of the terracelike folds on the cephalon but differs from them in higher eyes, absence of eye lists and the lingula of the cranidium, convex occipital ring, presence of an occipital furrow and terracelike folds on the occipital ring, and in the coarsely segmented rachis of the pygidium; additionally, from *A. heckeri*, it differs in higher eyes, which are more remote from the posterior margin of the cephalon and in the absence of tubercles from the posterolateral corners of the ocular areas. From *A. striatus*, it differs in shorter cephalon and pygidium, absence of rudiments of the glabellar lobe, marginal bend of the anterior branch of the facial suture being angular, convex occipital ring, coarsely segmented pygidial rachis, and in the presence of the terracelike folds on the anterior margin of the frontal lobe.

**Occurrence.** Middle Ordovician, Llanvirn, Kunda Horizon, upper part of the *sulevi-ingrianus* Zone; Simankovo Formation, upper part of Member 1. Outside the Ladoga Glint: Baltic Glint, upper parts of the Sinyavino, Loobu, and Napa formations.

**Material.** Sixty-eight specimens: Volkhov River, 0.4–0.55 m below ds4; Lava River, Putilovo River.

*Asaphus laevis-simus* F. Schmidt, 1901

Plate 8, figs. 5 and 6; Plate 9, figs. 1–3; Plate 21, fig. 6

*Asaphus laevis-simus*: Schmidt, 1898, p. 24 (nom. nud.); 1901, p. 58 (part), pl. 5, figs. 1–6, 9, fig. 12(?), pl. 12, figs. 22 and 23 (non pl. 5, figs. 7, 7a, 8, 13 = *S. latisegmentatus* and pl. 5, fig. 11 = *S. laticaudatus* (?)); Lesnikova and Weber, 1949, p. 287, pl. 72, fig. 1.

*Asaphus* (*Neoasaphus*) *laevis-simus*: Jaanusson, 1953a, p. 398.

*Asaphus* (*Trematophorus*) *laevis-simus*: Balashova, 1953, p. 411, pl. 1, figs. 14, 16 (?), 28 (?), pl. 5, fig. 4.

*Asaphus* (*Subasaphus*) *laevis-simus*: Balashova, 1976, p. 10.

*Asaphus laevis-simus*: Ivantsov, 2000, figs. 1e and 1f.

**Neotype.** Specimens DPStPSU, no. 569/9243, designated and depicted by Balashova (1953, pl. 5, fig. 4), rolled carapace; Volkhov River, excavation of the Volkhov hydroelectric power station, 5 m above the upper lenticular bed, Volkhovstroï Subhorizon; collected by Yanishevskii, 1924.

**Diagnosis.** Cephalon medium-proportionate, with a sharp beaklike bend; glabella not reaching anterior margin; basal lobes lenslike; rudiments of glabellar lobes absent; occipital furrow absent or represented by pit; paradoublural furrows absent; cranidium with broad lingula; marginal bend of anterior branch of facial suture sharply angular; eyes medium long and high; removed from posterior end at distance little less than their length; eye pedicles absent; eye lists present; ocular areas not elevated above cephalon and barren of tubercles; occipital ring flat; pygidium shortened, with rounded lateral margins and rounded or slightly obtuse posterior end; rachis faintly subdivided; terracelike folds absent from anterior part of frontal lobe and librigenae.

**Description.** The carapace is medium-sized and large, the maximum measured width of the cephalon is 50 mm; mean d, 36.5 mm. The cephalon is medium-proportionate (mean l/d, 0.47), anteriorly acuminate, with a sharp beaklike bend. The frontal lobe of the glabella is strongly convex, with the maximum convexity in the posterior portion, not reaching far into the anterior margin, anteriorly bordered with a distinct furrow, and bears a longitudinal ridge. The medial lobe is weakly bordered laterally, the flexure between it and the frontal lobe is weak. The basal lobes are lenslike and weakly expressed. Rudiments of the glabellar lobes are absent. The eyes are medium-long and medium-high, moved to the posterior margin of the shield at a distance somewhat less than their length, approximated (mean lo/l, 0.28; mean ho/lo, 0.72; mean la/lp, 1.9; and mean do/d, 0.47). The eye socles are underdeveloped. The eye pedicles and tubercles in the posterolateral corners are absent. The eye lists are distinct. The ocular areas are not elevated above the cephalon. The bends in the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is sharp and angular, and the anterior one is distinct. The cranidium has a broad lingula. The distance between the facial

Explanation of Plate 9

**Figs. 1–3.** *Asaphus laevis-simus* F. Schmidt, 1901: (1) specimen PIN, no. 4330/47, rolled carapace,  $\times 1.5$ : (1a) dorsal view, (1b) frontal view, (1c) view from the frontal lobe, (1d) side view; Volkhov River, Volkhov power station dam outcrop; Kunda Horizon, Simankovo Formation, Member 2, *laevis-simus* Zone, 0.2 m below ds4; (2) specimen PIN, no. 4330/86, rolled, partially destroyed carapace of a large individual: (2a) pygidium,  $\times 1$ ; (2b, 2c) cephalon: (2b) dorsal view,  $\times 1$ ; (2c) side view,  $\times 1.5$ ; left bank of the Lava River, 100 m below the Kavra River mouth; same stratigraphical position and age, talus; (3) specimen PIN, no. 4330/85, rolled carapace of small specimen,  $\times 2$ : (3a) pygidium, (3b) cephalon; Volkhov River, Volkhov power station dam outcrop; same stratigraphical position and age; 0.15 m below ds4.

**Figs. 4–7.** *Asaphus heckeri* Ivantsov, 2000: (4) holotype PIN, no. 4330/48, rolled, slightly deformed carapace,  $\times 1.5$ : (4a) dorsal view, (4b) side view, (4c) frontal view, (4d) view from the frontal lobe, (4e) pygidium; Volkhov River, Volkhov power station dam outcrop; Aseri Horizon, Simankovo Formation, Member 3; *heckeri* Zone, talus; (5) specimen PIN, no. 4330/50, rolled, partially destroyed and deformed carapace,  $\times 1.5$ : (5a) dorsal view, (5b) frontal view; same age and locality, 0.35 m above ds4; (6) specimen PIN, no. 4330/49, rolled carapace fragment,  $\times 1.5$ ; same age and locality, 0.15 m above ds4; (7) specimen PIN, no. 4330/88, rolled carapace fragment,  $\times 1$ : (7a) dorsal view, (7b) half-turned view; village of Katlino by the town of Pavlovsk, stratigraphical position unknown; collected by S. Shevryev in 1900.

sutures at the level of the marginal bends is greater than such distance at the eye sockets. The maximum width of the anterior part of the fixed gena is situated near the anterior margin of the shield. The dorsal furrows are small on the frontal lobe and those of the basal lobes are small or absent. The glabellar furrows are small and fused with small and diffused pseudodorsal furrows. The occipital furrow is absent or developed as a small pit. The fossulae and paradoublural furrows are absent. The occipital node is distinct. The librigenae are flat. The genal corners are acuminate. The vincular pits are not expressed on the outer face. The occipital ring and rings of the body rachis are flat. The pygidium is shortened (mean L/D, 0.54), with rounded lateral margins and a rounded or slightly obtuse posterior end. The rachis is weakly segmented (up to three segments are visible on the carapace) and sharply bordered posteriorly. The pleurae are flattened, smooth, and lack a bordering posteriad of the rachis. The D-folds are weak, folds emphasizing segmentation are present on the rings of the body rachis and on the pygidial rachis.

**Variability.** The ontogenetic variability is mainly expressed in the increase of the relative width of the cephalon and pygidium. The variability is expressed in the relative width of the cephalon, the degree of development of the beaklike bend of the anterior margin, and the degree of approximation of the eyes.

**Comparison.** This species is similar to *A. heckeri* in the general shape of the cephalon, relatively low eyes, weakly developed occipital furrow, sharp marginal bend of the anterior branch of the facial suture, presence of the lingula of the cranidium and the eye lists, flat occipital ring, shortened pygidium possessing a weakly segmented rachis, and weak development of the terracelike folds, but differs in the eyes being relatively higher and shifted farther from the posterior margin of the cephalon, in the absence of tubercles from the posterolateral corners of the ocular areas and terracelike folds from the frontal lobe. The comparison with *A. lepidurus*, *A. raniceps*, and *A. ingrianus* is given under their description.

**Remarks.** Schmidt's specimen (1901, pl. 5, figs. 7, 7a) designated by Balashova as the lectotype (Balashova, 1953) and holotype (Balashova, 1976) has not survived and apparently does not belong to this species. Judging from the low eyes and the gentle flexure between the eye socle and the librigena, its assignment to the genus *Subasaphus* is more probable.

Balashova (1976) mentioned the presence of subasaphine panderian organs in this species, which is apparently erroneous. In our and Balashova's collections, all and rather numerous cephalons that have been prepared possess the panderian organs developed as slotlike incisions.

Schmidt (1901) united *A. laevissimus* and *S. laticaudatus* under a single specific name. These species are similar to each other in the same shape of the cephalon, which is wide in large individuals of *A. laevissimus* and acuminate anteriorly, in the relatively low eyes, weak development of the glabellar and occipital furrows, flat

occipital ring, flat rings of the body rachis, weakly expressed terracelike folds, and a pygidium shortened and obtuse posteriorly. The species under description differs from *S. laticaudatus* in shorter and higher, heavily approximated eyes with well-developed eye lists, in the absence of (specific for *S. laticaudatus*) a gentle transition from the eye optic surface to the librigena, in the flat posterior parts of the librigenae, absence of terracelike folds on the frontal lobe, shorter pygidium, and the neosaphine panderian organs.

**Occurrence.** Middle Ordovician, Llanvirn, Kunda Horizon, the *laevissimus* Zone; Simankovo Formation, Member 2. Outside the Ladoga Glint: Baltic Glint, upper parts of the Sinyavino, Loobu, and Napa formations. According to Balashova and Rõõmusoks, this species is also recorded in Estonia, near Luga, village of Aseri, and on the Purtse River (Balashova, 1953, 1976; Rõõmusoks, 1960). A form identified as *A. cf. laevissimus* is found on the northwestern slope of the Belorussian Massif (Ilgai-56 borehole, lower part of the Miory Formation (Lashkov *et al.*, 1983)) and in northeastern Poland (Modlinski, 1973).

**Material.** One hundred and sixty-seven specimens: Volkhov River, 0.02–0.35 m below ds4; Lava River, 0.05–0.25 m below ds4; village of Putilovo.

*Asaphus heckeri* Ivantsov, 2000

Plate 9, figs. 4–7

*Asaphus heckeri*: Ivantsov, 2000, p. 50, pl. 9, fig. 1, text-fig. 1c and 1d.

**Holotype.** PIN, no. 4330/48, rolled carapace; Volkhov River, Volkhov hydroelectric power station dam outcrop (Fig 13); Middle Ordovician, Llanvirn, Aseri Horizon, Simankovo Formation, Member 3; *heckeri* Zone, talus (Pl. 9, fig. 4).

**Diagnosis.** Cephalon shortened, with weak beaklike bend; glabella not reaching anterior margin; basal lobes lenslike; rudiments of glabellar lobes present; occipital furrow pitlike; paradoublural furrows absent; cranidium acuminate anteriorly; marginal bend of anterior branch of facial suture sharply angular; eye medium-long, low, removed from posterior margin at half length of eye; eye pedicles absent; eye lists present; ocular areas not elevated above cephalon, possess tubercles; occipital ring flat; pygidium shortened, with rounded lateral margins and posterior end; rachis faintly subdivided; terracelike folds present on anterior part of frontal lobe and absent from librigenae.

**Description.** The carapace is medium-sized, the maximum measured width of the cephalon is 36 mm. Cephalon shortened (mean l/d, 0.45), anteriorly acuminate, with weak beaklike bend. The frontal lobe is moderately convex, with the maximum convexity in the middle part, not reaching the anterior margin, abruptly bordered anteriorly, and lacking a longitudinal ridge. The medial lobe is weakly bordered laterally, the flexure between it and the frontal lobe is weak. The basal lobes are lenslike and weakly defined. Rudiments of the glabellar lobes are present. The eyes are medium-

long, low, approximated to the posterior margin at about half a length of the eye, moderately separated (mean  $lo/l$ , 0.33; mean  $ho/lo$ , 0.53; mean  $la/lp$ , 2.5; and mean  $do/d$ , 0.53). The eye socles are underdeveloped. The eye pedicles are absent. The eye lists are weakly defined. The ocular areas are not elevated above the shield. The tubercles in the posterolateral corners of the ocular areas are distinct. The bends in the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is sharp and angular, and the anterior one is distinct. The cranium has a small lingula. The distance between the facial sutures at the level of the marginal bends is greater than such a distance at the eye socles. The maximum width of the anterior part of the fixed gena is situated near the anterior margin. The dorsal furrows are distinct on the frontal lobe and weakly expressed on the basal lobes. The pseudodorsal furrows are wide and shallow. The glabellar furrows are shallow. The occipital furrow is pitlike. The fossulae are unclear. The paradoublural furrows are absent. The occipital node is distinct. The librigenae are concave in their posterior parts. The genal corners are acuminate. The vincular pits are not expressed on the outer surface. The occipital ring and the rings of the body rachis are flat. The pygidium is shortened (mean  $L/D$ , 0.52), with rounded lateral margins and a posterior end. The rachis is weakly segmented along its entire length (up to eight segments are visible) and abruptly bordered posteriorly. The pleurae are flat, smooth, lacking a bordering posteriad of the rachis. The D-folds are weak on the anterior margin of the frontal lobe of the glabella and on the anterolateral margins of the pygidial pleurae. The panderian organs are neosaphine.

The comparison with *A. ingrianus* and *A. laevisimus* is given under their description.

**Remarks.** This species is similar to the stratigraphically close earlier representatives of the genus *Subasaphus*, *S. latisegmentatus* and *S. laticaudatus* (see Remarks section under the description of the latter species).

**Occurrence.** Middle Ordovician, Llanvirn, Aseri Horizon, *heckeri* Zone; Simankovo Formation, lower part of Member 3. Outside the Ladoga Glint: Baltic Glint, Duboviki Formation, Aseri (?) Formation (specimens TMN, no. 91/5197).

**Material.** Sixteen specimens: Volkhov River, 0–0.35 m above ds4; Lava River, 0.05 m above ds4.

***Asaphus kotlukovi* Balashova, 1953**

Plate 10, figs. 1–7

*Asaphus cornutus*: Schmidt, 1901, p. 47 (part.), pl. 4, fig. 1; Lesnikova and Weber, 1949, pl. 70, fig. 3.

*Asaphus (Trematophorus) kotlukovi*: Balashova, 1953, p. 407, pl. 1, fig. 26 (?), pl. 4, figs. 8–11.

*Asaphus (Neosaphus) kotlukovi*: Balashova, 1976, p. 16.

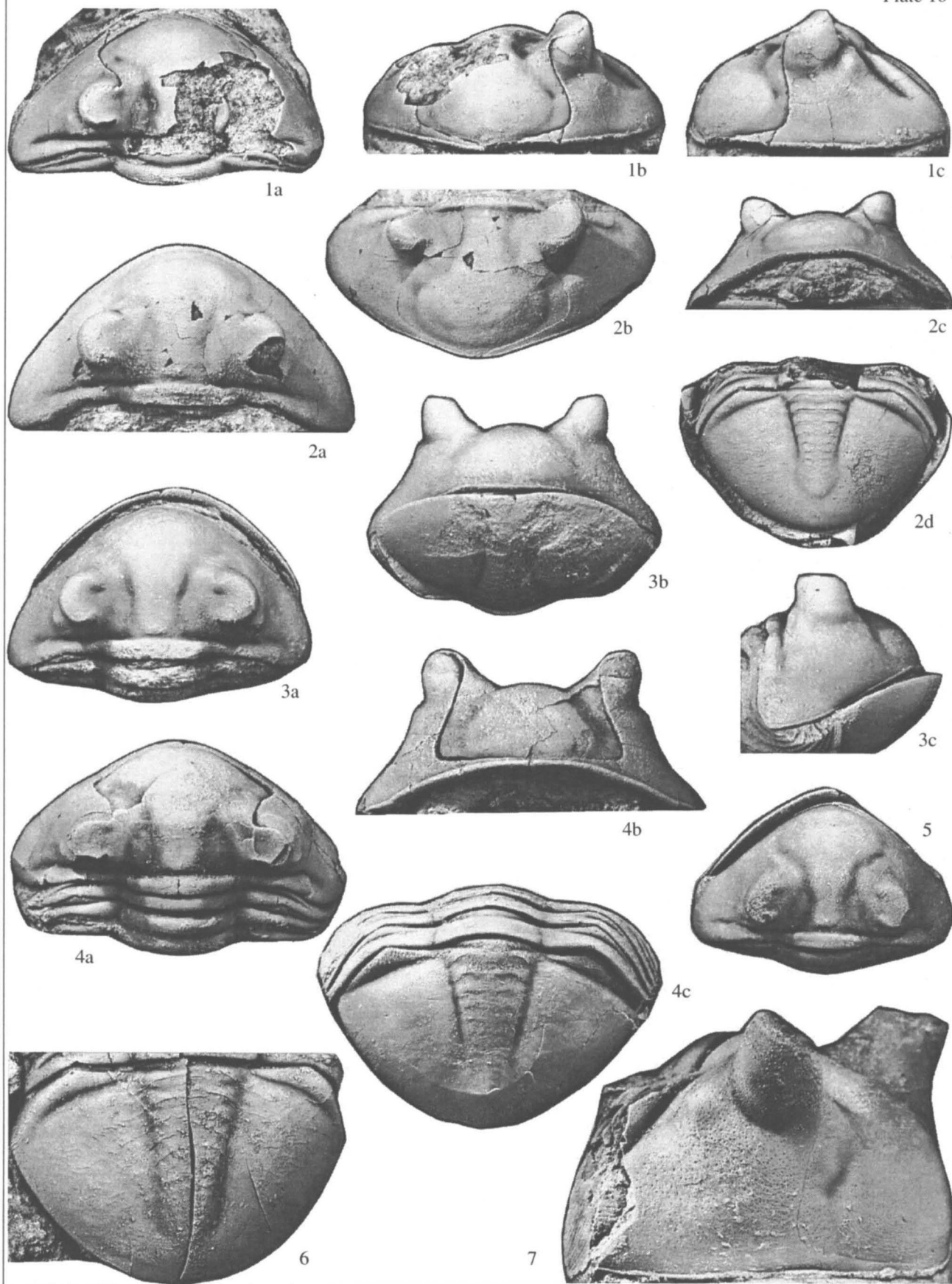
*Asaphus kotlukovi*: Ivantsov, 2000, fig. 1a and 1b.

**Holotype.** DPStPSU, no. 590/9243, cephalon with partially destroyed carapace, designated and

depicted by Balashova (1953, pl. 4, figs. 10, 11); Volkhov River; Volkhovstroi Subhorizon (Pl. 10, fig. 1). The number mentioned in Balashova's paper does not match the specimen's label.

**Diagnosis.** Cephalon medium-proportionate or shortened, with weak beaklike bend or without it; glabella reaching anterior margin; basal lobes lenslike; rudiments of glabellar lobes absent; occipital furrow deep; paradoublural furrows absent; cranium anteriorly acuminate or with small lingula; marginal bend of anterior branch of facial suture rounded or angular; eyes elongated, medium-long and medium-high, removed from posterior margin for less than their eye length; eye pedicles absent; eye lists present; ocular areas not elevated above cephalon or convex, with tubercles; occipital ring convex; pygidium shortened, with rounded lateral margins and posterior end; rachis coarsely segmented; terracelike folds present on the anterior part of the frontal lobe and rarely present on the librigenae.

**Description.** The carapace is medium-sized, rarely large, the maximum measured width of the cephalon is 55 mm; mean  $d$ , 41.5 mm. The cephalon is medium-proportionate or shortened (mean  $l/d$ , 0.45–0.49), weakly acuminate anteriorly, with a weak beaklike bend or without it. The frontal lobe is moderately convex, with the maximum convexity in the middle part, reaching the anterior margin, weakly bordered anteriorly, and lacking a longitudinal ridge. The medial lobe is clearly bordered laterally, the flexure between it and the frontal lobe is weak or absent. The basal lobes are lenslike and weakly defined. Rudiments of the glabellar lobes are absent. The eyes are elongated, medium-high and high, approximated to the posterior margin at a distance a little less than their length, widely or moderately separated (mean  $lo/l$ , 0.34–0.35; mean  $ho/lo$ , 0.8–0.94; mean  $la/lp$ , 1.7–1.8; and mean  $do/d$ , 0.55–0.59). The eye socles are fully developed. The eye pedicles are absent. The ocular areas are not elevated or convex. The eye lists are present. The tubercles in the posterolateral corners of the ocular areas are distinct. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded or angular, the anterior one is absent or just outlined. The cranium is acuminate anteriorly or has a faintly visible lingula. The distance between the facial sutures at the level of the marginal bends is greater than such a distance at the eye socles. The anterior part of the fixed gena is parallel-sided or strongly widened on the anterior side of the ocular list. The dorsal furrows are deep on the frontal lobe and faint on the basal lobes. The glabellar lobes are medium-deep and fused with medium-deep pseudodorsal furrows. The occipital furrow is deep. The fossulae are diffused or absent. The paradoublural furrows are absent. The occipital node is diffused or absent. The librigenae are concave in their posterior parts. The genal corners are acuminate to rounded. The vincular pit is not expressed on the outer surface or marked with hardly visible bends of the shield margin. The occipital



ring and rings of the body rachis are convex. The pygidium is medium-proportionate (mean L/D, 0.59–0.61), with rounded lateral and posterior margins. The rachis is coarsely segmented (up to eight segments are visible), posteriorly weakly bordered to diffused. The pleurae are convex, smooth, and lack bordering behind the rachis. The D-folds are weak; on the cephalon, they usually present on the anterior margin of the frontal lobe only; on the outer sides of the ocular areas, they are developed as exceptions only, the rest of the surface is barren of them; on rings of the body rachis, these folds are weak or absent; on the pygidial rachis, they are both those emphasizing segmentation and intercalary or emphasizing segmentation only; on the pleurae, these folds are radial and transverse. The librigenae are covered with rare deep pits. The panderman organs are neosaphine.

**Variability.** Juvenile individuals of this species have lower and relatively large eyes and the librigenae is less concave in their posterior parts.

**Subspecies included.** *A. kotlukovi kotlukovi* Balashova, 1953 and *A. kotlukovi tumidus* subsp. nov.

**Comparison.** This species is similar to *A. ingrianus*, *A. punctatus*, *A. cornutus*, and young individuals of *A. plautini* in the short cephalon, more or less sharp marginal bends of the anterior branches of the facial sutures, and in the presence of the terracelike folds on the anterior part of the frontal lobe; it differs from *A. ingrianus* in the eyes being large and situated closer to the posterior margin of the cephalon, in the presence of the eye lists and tubercles in the posterolateral corners of the ocular areas, the ocular areas being occasionally convex, a deeper occipital furrow, and sometimes in the presence of the terracelike folds on the librigenae; from *A. punctatus*, it differs in lower eyes possessing no traces of the eye pedicles, more strongly developed tubercles in the posterolateral corners of the ocular areas, and in a shorter pygidium possessing the coarsely segmented rachis; from *A. cornutus*, it differs in the absence of paradoublural furrows, shorter pygidium with rounded lateral margins and the posterior end, more strongly segmented rachis, and weaker terracelike folds on the genae; from *A. plautini*, it differs in the high eyes, the presence of eye lists, stronger developed

tubercles in the posterolateral corners of the ocular areas, higher elevated ocular areas, the absence of paradoublural furrows, a deep occipital furrow, convex occipital ring, and a shorter pygidium with coarsely segmented rachis. The comparison with *A. sulevi* and *A. botnicensis* is given under their description.

**Occurrence.** Baltic-Ladoga Glint; Middle Ordovician, Llanvirn, Aseri Horizon, lower part of the *kotlukovi-punctatus* Zone.

*Asaphus kotlukovi kotlukovi* Balashova, 1953

Plate 10, figs. 1 and 2

*Asaphus (Trematophorus) kotlukovi*: Balashova, 1953, pl. 4, figs. 8–11.

*Asaphus (Neoasaphus) kotlukovi*: Balashova, 1976, p. 16.

*Asaphus kotlukovi*: Ivantsov, 2000, figs. 1a and 1b.

**Holotype.** The type of the species.

**Diagnosis.** Cephalon shortened, beaklike bend present; eyes medium-high; ocular areas not elevated above cephalon; marginal bend of anterior branch of facial suture rounded; pygidial rachis weakly bordered posteriorly; in cephalon, terracelike folds present on anterior side of glabella only.

**Comparison.** Differs from *A. kotlukovi tumidus* in a shorter cephalon (mean l/d, 0.45), the presence of a beaklike bend, ocular areas, which are almost not elevated above the cephalon, lower eyes (mean ho/lo, 0.8), a rounded marginal bend of the anterior branch of the facial suture, the pygidial rachis being distinctly bordered posteriorly, and in the absence of terracelike folds on the outer sides of the ocular areas.

**Occurrence.** Middle Ordovician, Llanvirn, Aseri Horizon, lower part of the *kotlukovi-punctatus* Zone; upper part of Member 3 of the Simankovo Formation. Outside the Ladoga Glint: Baltic Glint, lower part of the Duboviki or Aseri formations.

**Material.** Fifteen specimens: Volkhov River, 1.55–1.65 m above ds4; village of Putilovo.

*Asaphus kotlukovi tumidus* subsp. nov.

Plate 10, figs. 3–7

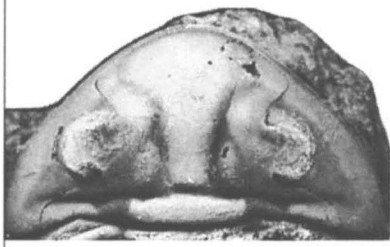
*Asaphus cornutus*: Schmidt, 1901, pl. 4, fig. 1.

**Etymology.** From Latin *tumidus* (swollen).

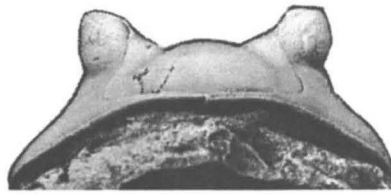
Explanation of Plate 10

**Figs. 1 and 2.** *Asaphus kotlukovi kotlukovi* Balashova, 1953: (1) holotype DPStPSU, no. 590/9243, cephalon with partially destroyed carapace,  $\times 2$ : (1a) dorsal view, (1b) view from the frontal lobe, (1c) half-turned view; Volkhov River; Volkhovstroï Sub-horizon, collected by Yanishevskii, 1923; (2) specimen PIN, no. 4330/106, rolled carapace: (2a–2c) cephalon: (2a) dorsal view,  $\times 2$ ; (2b) view from the frontal lobe,  $\times 2$ ; (2c) frontal view,  $\times 1.5$ ; (2d) pygidium,  $\times 1.5$ ; right bank of the Ruditsy River near the village of Lopukhinka; Aseri Horizon, Duboviki Formation, lower part of the *kotlukovi-punctatus* Zone, 1 m above the floor of the formation.

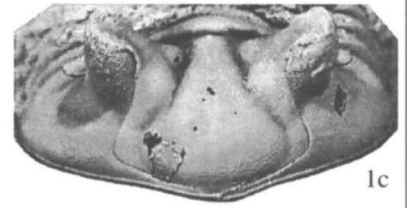
**Figs. 3–7.** *Asaphus kotlukovi tumidus* subsp. nov.: (3) specimen PIN, no. 4330/99, rolled carapace of small specimen,  $\times 2$ : (3a) dorsal view, (3b) frontal view, (3c) side view; Volkhov River, Volkhov power station dam outcrop; same stratigraphical position and age, 2.35 m above ds4; (4) holotype PIN, no. 4330/56, bent carapace,  $\times 1.5$ : (4a, 4b) cephalon: (4a) dorsal view, (4b) frontal view; (4c) pygidium; left bank of the Lava River, about 100 m below the Kavra River mouth; same stratigraphical position and age, talus; (5) specimen PIN, no. 4330/98, cephalon,  $\times 1.5$ ; Volkhov River, Volkhov power station dam outcrop; Aseri Horizon, Duboviki Formation; collected by Yanishevskii; (6) specimen PIN, no. 4330/94, pygidium,  $\times 1.5$ ; village of Putilovo, Aseri Horizon, Duboviki Formation, lower part of the *kotlukovi-punctatus* Zone, talus; (7) specimen PIN, no. 4330/96, cephalon half-turned view, judging from the development of the terracelike folds, this specimen takes an intermediate position between *A. kotlukovi* and *A. cornutus*,  $\times 5$ ; environs of the village of Krasnoe Selo; same stratigraphical position and age, talus.



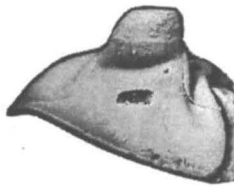
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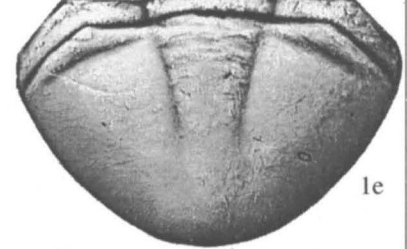
1b



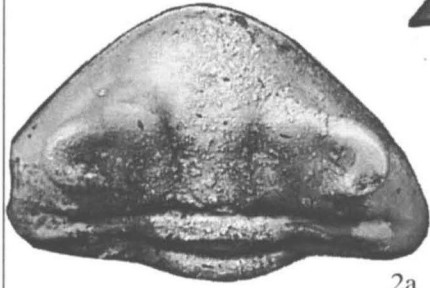
1c



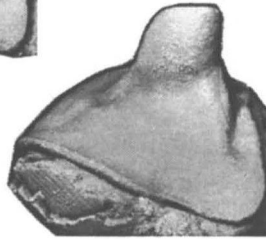
1d



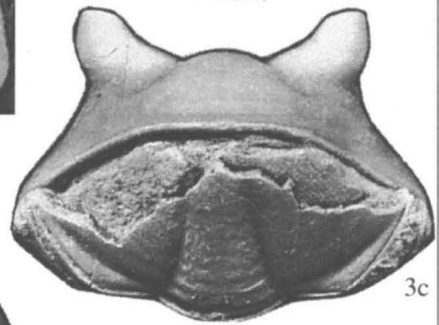
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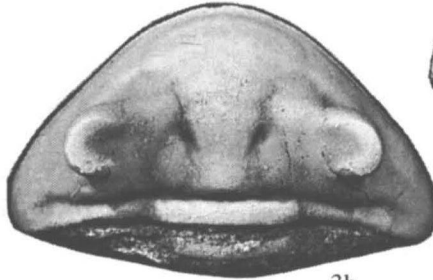
2a



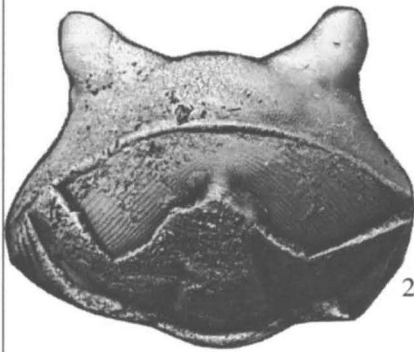
3a



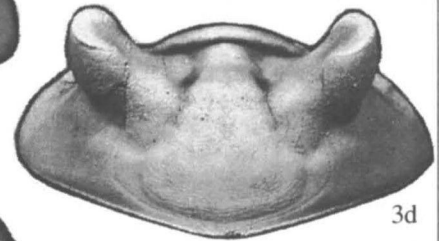
3c



3b



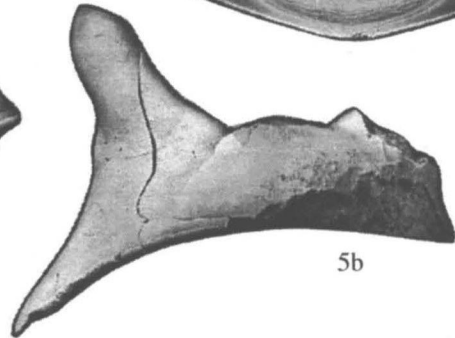
2b



3d



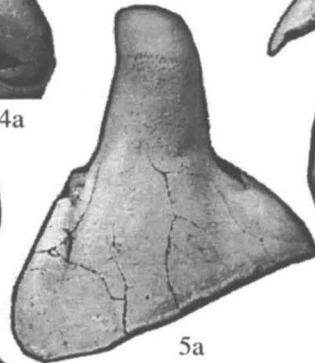
4c



5b



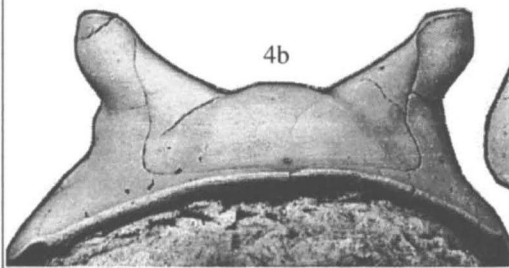
4a



5a



5c



4b

**H o l o t y p e.** PIN, no. 4330/56, rolled carapace; left bank of the Lava River, about 100 m downstream of the Kavra River mouth; Aseri Horizon, Duboviki Formation; *kotlukovi-punctatus* Zone, talus (Pl. 10, fig. 4).

**D i a g n o s i s.** Cephalon medium-proportionate, beaklike bend absent; ocular areas highly elevated; eyes high; marginal bend of anterior branch of facial suture angular; pygidial rachis diffused posteriorly; in cephalon, terracelike folds present on anterior side of glabella and occasionally on lateral slopes of ocular areas.

**C o m p a r i s o n.** The comparison with *A. kotlukovi* *kotlukovi* is given under the description of the latter species.

**R e m a r k s.** In this subspecies, I include a form with relatively low eyes and weak terracelike folds on the outer sides of the ocular areas as well. On the basis of these characters, it is transitional between *A. kotlukovi* and *A. cornutus*. See also Remarks section under the description of *A. punctatus*.

**O c c u r r e n c e.** Middle Ordovician, Llanvirn, Aseri Horizon, lower part of the *kotlukovi-punctatus* Zone; upper part of Member 3 of the Simankovo Formation.

Outside the Ladoga Glint: Baltic Glint, lower part of the Duboviki or Aseri formations.

**M a t e r i a l.** One hundred and seventy-five specimens: Volkhov River, 1.7–2.45 m above ds4 or 6.35–7.1 m below the floor of the Porogi Formation; Lava River, 2–3 m above ds4 or 5.6–6.6 m below the floor of the Porogi Formation; village of Putilovo.

#### *Asaphus punctatus* Lesnikova, 1949

Plate 11, figs. 1–5

*Asaphus cornutus* var. *punctatus*: Lesnikova and Weber, 1949, p. 283, pl. 70, figs. 2a and 2b.

*Asaphus (Trematophorus) punctatus*: Balashova, 1953, p. 408, pl. 4, figs. 1–6.

*Asaphus (Neoasaphus) punctatus*: Balashova, 1976, p. 18.

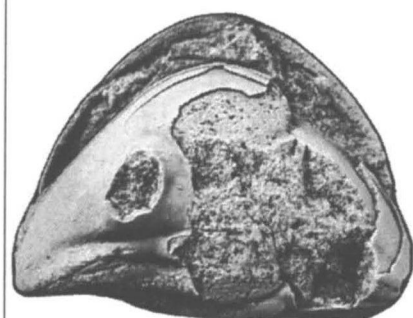
**H o l o t y p e** (monotype). DPStPSU, no. 580/9243, rolled, partially destroyed carapace, depicted by Lesnikova (Lesnikova and Weber, 1949; pl. 70, figs. 2a, 2b) and Balashova (1953; pl. 4, figs. 1–3); Volkhov River, Volkhovskroi Formation (Pl. 11, fig. 2). The number indicated in Balashova's paper does not match the specimen's label.

**D i a g n o s i s.** Cephalon medium-proportionate, without beaklike bend, glabella not reaching anterior margin; basal lobes lenslike; rudiments of glabellar lobes absent; occipital furrow deep; paradoublar furrows absent; cranidium with broad short lingula; marginal bend of anterior branch of facial suture rounded; bend of eye base reverse; eyes medium-long, high, removed from posterior margin for about half of their length; eye pedicles short and thick; eye lists present; ocular areas not elevated above cephalon or convex, with tubercles; occipital ring convex; pygidium medium-proportionate or weakly elongated; with rounded lateral margins and posterior end, rachis faintly subdivided; terracelike folds present on anterior part of frontal lobe and absent from librigenae.

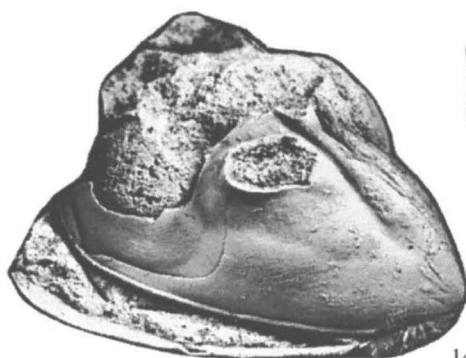
**D e s c r i p t i o n.** The carapace is medium-sized, the maximum measured width of the cephalon is 45.7 mm; mean d, 30.5 mm. The cephalon is medium-proportionate (mean l/d, 0.48–0.5), anteriorly acuminate, without beaklike bend. The frontal lobe is weakly to moderately convex, with the maximum convexity in the middle part, not reaching the anterior margin, weakly bordered anteriorly with a furrow, and lacking a longitudinal ridge. The medial lobe is clearly bordered laterally, the flexure between it and the frontal lobe is sharp. The basal lobes are lenslike and weakly defined. Rudiments of the glabellar lobes are absent. The eyes are medium-long, high, approximated to the posterior margin for approximately their length, widely separated (mean la/lp, 1.4–1.6; mean do/d, 0.63). The eye socles are fully developed. The eye pedicles are just outlined to medium-high, thicker than the eye socles. The ocular areas are not elevated or convex. The eye lists are present. Tubercles in the posterolateral corners of the ocular areas are weak but distinct. The bends of the anterior branch of the facial suture are as follows: the ocular bend is weak to sharp, the marginal bend is more or less rounded, and the anterior one is distinct. The cranidium has a short and wide lingula. The distance between the facial sutures at the level of the marginal bends is either less than, or greater than, or equal to such a distance at the eye socles. The anterior part of the fixed gena is widest on the anterior side of the ocular ridge. The dorsal furrows are shallow on the frontal and basal lobes. The glabellar furrows are deep and fused with pseudodorsal furrows. The occipital furrow

#### Explanation of Plate 11

**Figs. 1–5.** *Asaphus punctatus* Lesnikova, 1949: (1) specimen PIN, no. 4330/51, bent carapace,  $\times 2$ : (1a–1d) cephalon: (1a) dorsal view, (1b) frontal view, (1c) view from the frontal lobe, (1d) side view, (1e) pygidium; left bank of the Volkhov River, near the railroad bridge in the town of Volkhov; Aseri Horizon, Duboviki Formation, upper part of the *kotlukovi-punctatus* Zone, 2.35 m above ds4; (2) holotype DPStPSU, no. 580/9243, rolled, partially destroyed carapace,  $\times 1.5$ : (2a) dorsal view, (2b) frontal view; Volkhovskroi Formation; collected by Yanishevskii in 1921; (3) specimen PIN, no. 4330/57, rolled, partially destroyed carapace,  $\times 2$ : (3a) lateral view, (3b) dorsal view, (3c) frontal view, (3d) view from the frontal lobe; Ruditsa River near the village of Lopukhinka; Aseri Horizon, Duboviki Formation, upper part of the *kotlukovi-punctatus* Zone, talus; (4) specimen PIN, no. 4330/58, bent carapace of large individual,  $\times 1.5$ : (4a) dorsal view, (4b) frontal view, (4c) side view; left bank of the Volkhov River, near the railroad bridge in the town of Volkhov; same stratigraphical position and age, talus; (5) specimen PIN, no. 4330/64, bent, partially destroyed carapace,  $\times 1.5$ : (5a, 5b) cephalon: (5a) lateral view, (5b) frontal view; (5c) pygidium; right bank of the Ruditsy River near the village of Lopukhinka; same stratigraphical position and age, about 1.9 m above the floor of the formation.



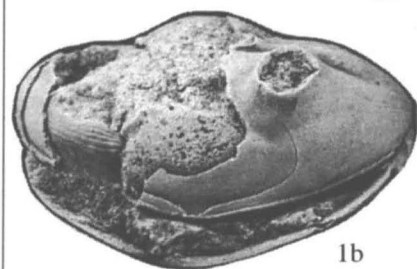
1a



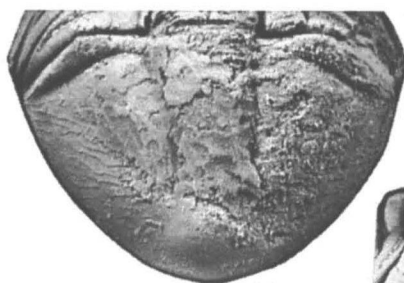
1c



2a



1b



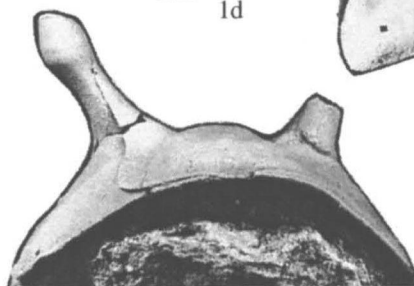
1d



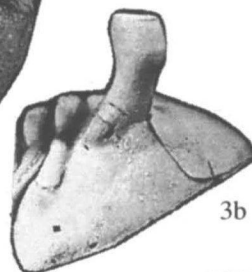
2b



3a



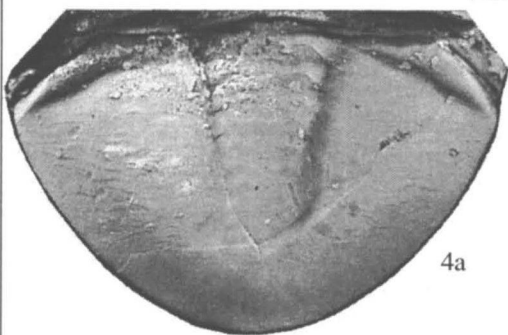
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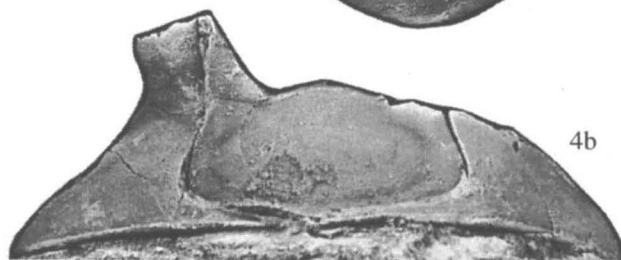
3b



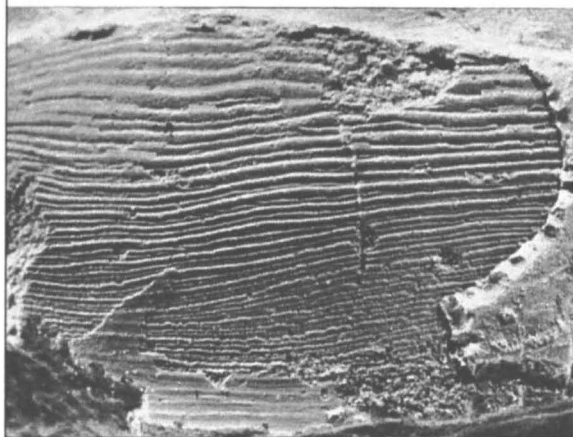
3d



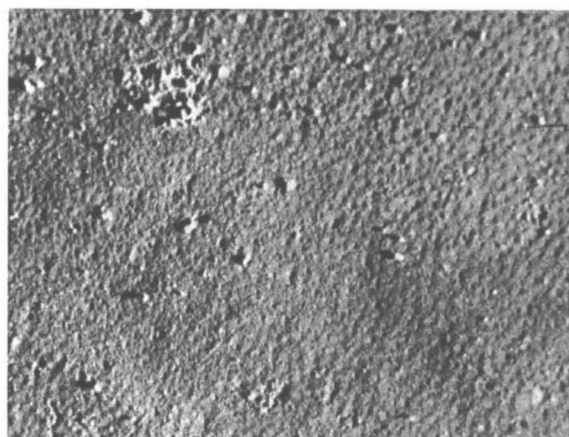
4a



4b



5



6

is deep. The fossulae are unclear. The paradoublural furrows are absent. The occipital node is unclear. The librigenae are concave in their posterior parts. The genal corners are rounded. The vincular pits are not expressed on the outer surface or marked by very faint bends of the shield margin. The occipital ring and rings of the body rachis are convex. The pygidium is medium-proportionate or weakly elongated (mean L/D, 0.59–0.62), with rounded lateral and posterior margins. The rachis is weakly segmented (three or four segments are visible), weakly bordered posteriorly. The pleurae are flattened to weakly convex, smooth, lacking a bordered posteriad of the rachis. The D-folds are weak, emphasizing segmentation and intercalary on the anterior margin of the frontal lobe and pygidial rachis and transverse on the pleurae. The pandertian organs are neosaphine.

Variability is expressed in the degree of the ocular area elevation and the development of eye pedicles that may be very high and thick (Pl. 11, fig. 5).

**Comparison.** This species is similar to *A. intermedius* in the same shape of the cephalon, high eyes, presence of eye pedicles, deep occipital furrow, a cranidium possessing short and wide lingula, a convex occipital ring, an elongated pygidium with weakly segmented rachis, and in the absence of the terracelike folds from the librigenae; it differs in shorter and thicker eye pedicles, the presence of tubercles in the posterolateral corners of the ocular areas, the absence of the paradoublural furrows, a rounded posteriorly pygidium, and in the absence of the terracelike folds from the genae. The comparison with *A. cornutus* and *A. kotlukovi* is given under their description.

**Remarks.** The name *Asaphus cornutus* var. *punctatus* was given by Lesnikova to one of the *A. cornutus* varieties by the presence of coarse pits on the librigenae. However, a specimen without this character was selected as the type specimen in the first publication, which appeared after the death of Lesnikova (Lesnikova and Weber, 1949). Later, based on this specimen (monotype) Balashova raised the rank of the variety to specific; as a result, the nominative feature was assigned to other species, *A. kotlukovi*. The only speci-

men depicted in the original paper has survived and should be treated as the holotype, not lectotype as proposed by Balashova (1953).

**Occurrence.** Middle Ordovician, Llanvirn, Aseri Horizon, upper part of the *kotlukovi*-*punctatus* Zone, lower part of the Duboviki Formation. Outside the Ladoga Glint: Baltic Glint, middle part of the Duboviki Formation, Aseri Formation; northwestern slope of the Belorussian Massif, Ilgai-56 borehole, lower half of the Miory Formation (Lashkov *et al.*, 1983).

**Material.** Thirty-six specimens: Volkhov River, 2.6–3.45 m above ds4 or 5.4–6.25 m below the floor of the Porogi Formation; Lava River, 3.3–3.4 m above ds4 or 5.2–5.3 m below the floor of the Porogi Formation.

#### *Asaphus intermedius* Balashova, 1953

Plate 12, figs. 1–3

*Asaphus (Trematophorus) intermedius*: Balashova, 1953, p. 409, pl. 4, figs. 12–15.

*Asaphus (Neosaphus) intermedius*: Balashova, 1976, p. 18.

**Holotype.** DPStPSU, no. 554/9243, unrolled, partially destroyed carapace, Balashova depicted (1953, pl. 4, fig. 12) and designated it (Balashova, 1976); village of Kopor'e; Volkhovstroi Subhorizon (Pl. 12, fig. 2). The number mentioned in Balashova's papers does not match the specimen's label.

**Diagnosis.** Cephalon medium-proportionate, with or without weak beaklike bend; glabella not reaching far anterior margin; basal lobes lenslike; rudiments of glabellar lobes absent; occipital furrow deep; paradoublural furrows weak; cranidium with broad and short lingula; marginal bend of anterior branch of facial suture rounded; bend of eye base reverse; eyes medium-long, high, approximated to posterior margin; eye pedicles long and thin; eye lists present; ocular areas not elevated above cephalon and barren of tubercles; occipital ring convex; pygidium elongated, with rounded lateral margins and acuminate posterior end; rachis faintly subdivided; terracelike folds present on anterior part of frontal lobe and occasionally on librigenae.

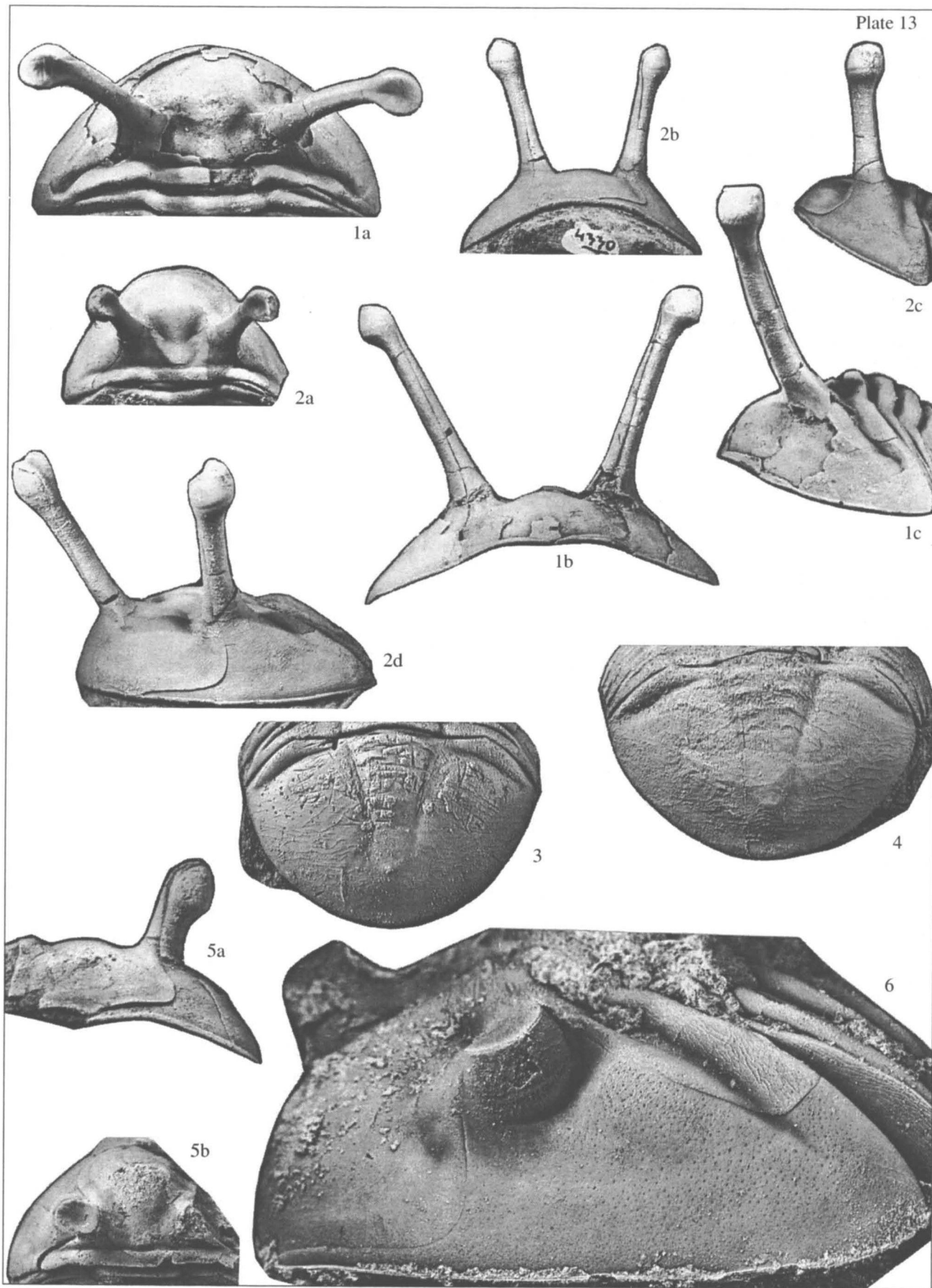
**Description.** The carapace is medium-sized and large, the maximum measured width of the cepha-

#### Explanation of Plate 12

**Figs. 1–3.** *Asaphus intermedius* Balashova, 1953: (1) specimen PIN, no. 4330/108, rolled, heavily destroyed carapace,  $\times 2$ : (1a) dorsal view, (1b) view from the frontal lobe, (1c) half-turned view, (1d) pygidium; Volkhov River, Volkhov town; Aseri Horizon, Duboviki Formation; collected by Lesnikova, 1930; (2) holotype DPStPSU, no. 554/9243, unrolled carapace fragment,  $\times 2$ : (2a) pygidium, (2b) cephalon, lateral view; village of Kopor'e; Volkhovstroi Subhorizon; (3) specimen PIN, no. 4330/63, unrolled carapace,  $\times 1.5$ : (3a–3c) cephalon: (3a) dorsal view, (3b) side view, (3c) frontal view, (3d) pygidium; Volkhov River, Duboviki outcrop; Aseri Horizon, Duboviki Formation, lower part of the beds with *A. intermedius*-*A. kowalewskii*, about 4.5 m above ds4.

**Fig. 4.** Transitional form between the species *Asaphus punctatus* and *Asaphus intermedius*, specimen PIN, no. 4330/179, rolled carapace fragment,  $\times 2.5$ : (4a) pygidium, (4b) cephalon frontal view; Volkhov River, Volkhov town, near the railroad bridge, Aseri Horizon, talus.

**Figs. 5 and 6.** *Asaphus knyrkoi* F. Schmidt, 1901: (5) specimen PIN, no. 4330/177, terracelike folds on the pygidial doublure (impression on mold),  $\times 5$ ; Putilovo outcrop, Kunda Horizon, Obukhovo Formation, Member 4, upper part of the *raniceps*-*striatus* Zone (with *A. striatus striatus*), 0.8 m below the roof of the member; (6) specimen PIN, no. 4330/33, fragment of outer surface of the cephalon carapace, tightly approximated large pits are visible,  $\times 15$ ; Volkhov River, Zvanka outcrop; same stratigraphical position and age, 5.3 m above the floor of the Obukhovo Formation.



lon is 48.3 mm. The cephalon is medium-proportionate (mean l/d, 0.51), anteriorly acuminate. The beaklike bend is absent or weak. The frontal lobe is weakly convex, with the maximum convexity in the middle part, not reaching the anterior margin, weakly bordered anteriorly, and bearing a longitudinal ridge. The medial lobe is clearly bordered laterally, the flexure between it and the frontal lobe is weak. The basal lobes are lenslike and moderately expressed. Rudiments of the glabellar lobes are absent. The eyes are medium-long, high, elevated on the long pedicles. The long axis of the transverse section of the eye pedicle is less than the long axis of the eye socle. The eye bases are approximated to the posterior margin of the shield, widely separated (mean lo/l, 0.27; mean ho/lo including eye pedicles, 2.2; mean la/lp, 2.5; and mean do/d, 0.59). The eye socles are fully developed. The ocular areas are not elevated above cephalon. The eye lists are present. Tubercles in the posterolateral corners of the ocular areas are absent. The bends in the anterior branch of the facial suture are as follows: the ocular bend is weak, the marginal bend is rounded, and the anterior one is distinct. The cranidium has a short and wide lingula. The distance between the facial sutures at the level of the marginal bends is considerably less than such distance at the eye socles. The maximum width of the anterior part of the fixed gena is situated on the anterior side of the eye list. The dorsal furrows on the frontal and basal lobes are weak. The glabellar furrows are deep and fused with deep pseudodorsal furrows. The occipital furrow is deep. The fossulae are unclear. The paradoublural furrows are weak. The occipital node is diffused. The librigenae are flat. The genal corners are rounded. The vincular pits are not expressed on the outer surface. The occipital ring and rings of the body rachis are convex. The pygidium is elongated (mean L/D, 0.73), with weakly rounded lateral margins and an acuminate posterior end. The rachis is weakly segmented (two or three segments are visible) and weakly bordered posteriorly. The pleurae are flat and smooth, a weak limblike flexure is developed behind the rachis. The D-folds are weak; transverse folds are developed on the anterior margin of the frontal lobe, on the librigenae near the anterior margin of the shield and on the outer sides of the ocular

areas (near the paradoublural furrows and near the genal corners, they are absent), and on the pygidial pleurae. The panderian organs are neoasaphine.

**Variability** is expressed in the development of terracelike folds on the librigenae which range from isolated stripes to a dense pattern.

**Comparison.** This species is similar to *A. kowalewskii* in the long and thin eye pedicles, absence of tubercles from the posterolateral corners of the ocular areas, rounded marginal bend of the anterior branch of the facial suture, presence of the lingula in the cranidium and of paradoublural furrows, deep occipital furrow, a convex occipital ring, a pygidium having rounded lateral margins and an acuminate posterior end; it differs in a long cephalon, lenslike form of the basal lobes, considerably shorter and somewhat thicker eye pedicles, weaker segmented pygidial rachis, and a smaller distribution of the terracelike folds over the librigenae. The comparison with *A. punctatus* is given under the description of the latter species.

**Remarks.** There is one specimen, which is transitional between the species under description and *A. punctatus* (Pl. 12, fig. 4). It has eye pedicles which are not as long as those of *A. intermedius*, but its pygidium is posteriorly acuminate. I assign it to the latter species with reservation.

**Occurrence.** Middle Ordovician, Llanvirn, Aseri Horizon, lower part of the *intermedius*-*kowalewskii* Beds; middle part of the Duboviki Formation. Outside the Ladoga Glint: Baltic Glint.

**Material.** Four specimens: Volkhov River, 4.45 m above ds4 or 4.4 m below the floor of the Porogi Formation; Lava River.

*Asaphus kowalewskii* Lawrow, 1856

Plate 13, figs. 1–5; Plate 21, figs. 7 and 8

*Asaphus kowalewskii*: Lawrow, 1856, p. 239, pl. 5, figs. a–c; Schmidt, 1901, p. 52–54, pl. 2, figs. 11–14, 16, and 17 (non fig. 15 = *Asaphus* ex gr. *cornutus*), pl. 12, figs. 16–18; Lesnikova and Weber, 1949, p. 283, pl. 70, fig. 1, pl. 72, fig. 4.

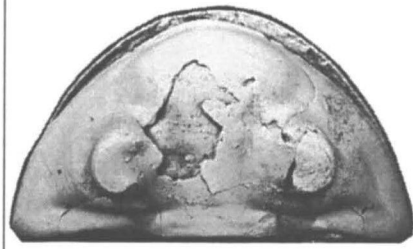
*Asaphus (Trematophorus) kowalewskii*: Balashova, 1953, p. 410, pl. 1, figs. 9 (?), 21 (?), pl. 4, fig. 16.

*Asaphus (Neoasaphus) kowalewskii*: Jaanusson, 1953a, p. 398; Balashova, 1976, p. 18.

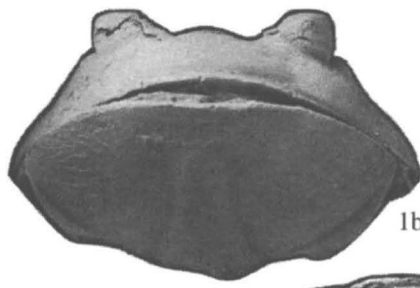
Explanation of Plate 13

**Figs. 1–5.** *Asaphus kowalewskii* Lawrow, 1856: (1) specimen PIN, no. 4330/111, cephalon of adult individual with maximally developed eye pedicles,  $\times 1.5$ : (1a) dorsal view, (1b) frontal view, (1c) side view; left bank of the Lava River near the northern outskirts of the village of Naziya; Aseri Horizon, Duboviki Formation, upper parts of the beds with *A. intermedius*-*A. kowalewskii*; (2) specimen PIN, no. 4330/61, cephalon: (2a) dorsal view,  $\times 1.5$ ; (2b) frontal view,  $\times 1.5$ ; (2c) side view,  $\times 1.5$ ; (2d) half-turned view,  $\times 2$ ; left bank of the Volkhov River near the new bridge of the town of Volkhov; same stratigraphical position and age, 6.65 m above ds4; (3) specimen PIN, no. 4330/150, elongated pygidium,  $\times 1.5$ ; left bank of the Volkhov River, Volkhov; same stratigraphical position and age; collected by M. Legeev; (4) specimen PIN, no. 4330/62, shortened pygidium,  $\times 1.5$ ; left bank of the Volkhov River, Volkhov, near the auto-bridge; same stratigraphical position and age, 6.55 m above ds4; (5) specimen PIN, no. 4330/109, fragment of the cephalon of a juvenile individual: (5a) frontal view,  $\times 3.5$ ; (5b) dorsal view,  $\times 2.5$ ; right bank of the Lava River near the northern outskirts of Naziya; same stratigraphical position and age.

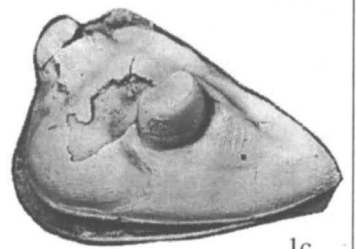
**Fig. 6.** *Asaphus lepidurus* Nieszkowskii, 1859, specimen PIN, no. 4330/67, sculpture of the dorsal side of the anterior part of the carapace; large pits, apertures of sensorial bristle pores are visible (Balashova, 1955), terracelike folds of the ocular field near the genal corner, along the posterior border, and at the first pleura of the body are also visible,  $\times 4$ ; Putilovo outcrop; Volkhov Horizon, Volkhov Formation, Frizy Member, the beds with *A. lepidurus*, dump.



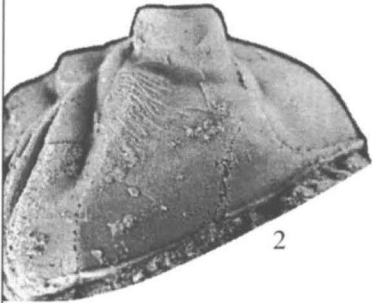
1a



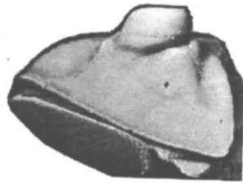
1b



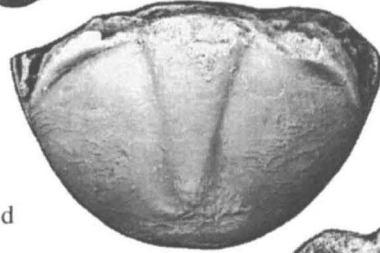
1c



2



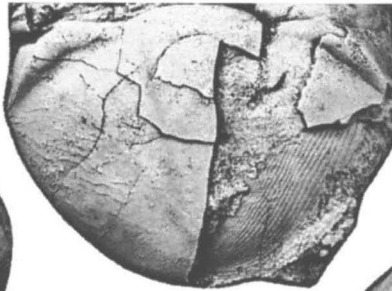
1d



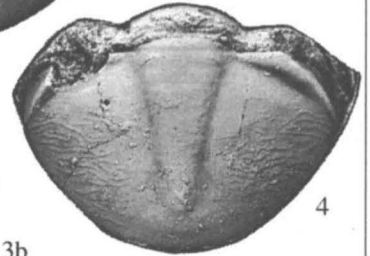
1e



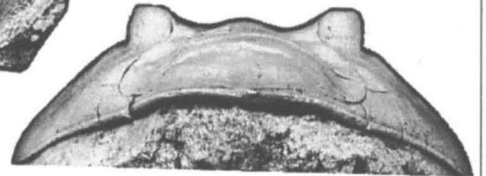
3a



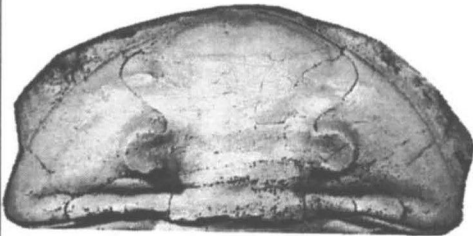
3b



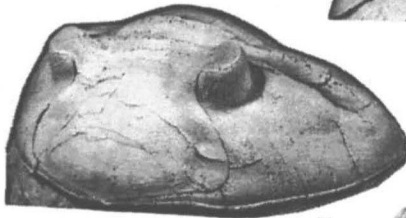
4



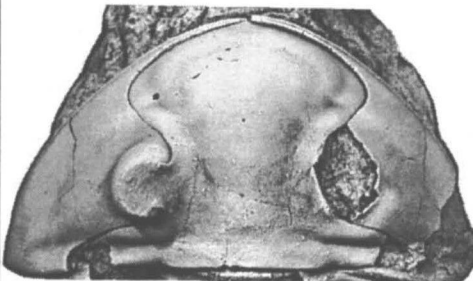
5c



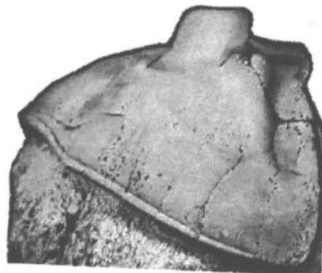
5a



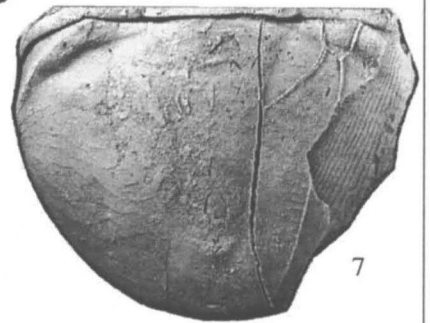
5b



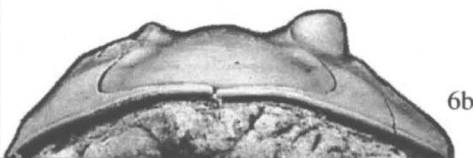
6a



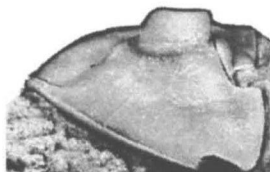
5d



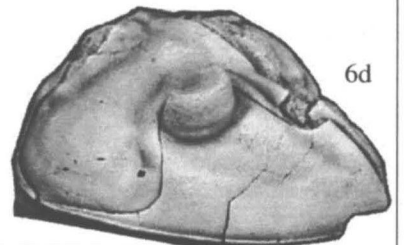
7



6b



6c



6d

**Neotype.** DPStPSU, no. 524/9243, rolled, partially destroyed carapace, designated and depicted by Balashova (1953, pl. 4, fig. 16); left bank of the Volkhov River, quarry near the ferry; Volkhovstroi Sub-horizon. The number mentioned in the cited paper does not match the specimen's label.

**Diagnosis.** Cephalon shortened, without beaklike bend, glabella not reaching anterior margin; basal lobes trapezoid; rudiments of glabellar lobes absent; occipital furrow deep; paradoublural furrows weak; cranidium with broad lingula; marginal bend of anterior branch of facial suture rounded; eyes medium-long, high, their bases close to posterior margin of cephalon; eye pedicles long and thin; eye lists absent; ocular areas not elevated above cephalon and devoid of tubercles; occipital ring convex; pygidium elongated, with rounded lateral margins and rounded or acuminate posterior end; rachis coarsely segmented; pleurae bordered at rear of rachis; terracelike folds on anterior part of frontal lobe and on librigenae present.

**Description.** The carapace is medium-sized and large, the maximum measured width of the cephalon is 49.5 mm; mean d, 39 mm. The cephalon shortened (mean l/d, 0.44), rounded anteriorly, without beaklike bend. The frontal lobe of the glabella is moderately convex, with the maximum convexity in the middle part, not reaching the anterior margin, not bordered with the preglabellar furrow, occasionally has a weak longitudinal ridge. The medial lobe is clearly bordered laterally, the flexure between it and the frontal lobe is sharp. The basal lobes are trapezoid and distinct. Rudiments of the glabellar lobes are absent. The eyes are of medium length, high, and elevated on high pedicles. The long axis of the transverse section of the eye pedicle is less than the long axis of the eye socle. The eye bases are close to the posterior margin of the shield and are widely separated (mean lo/l, 0.29; mean la/lp, 1.5; and mean do/d, 0.49). The eye socles are fully developed. The ocular areas are not elevated above the cephalon. The eye lists are absent. Tubercles in the posterolateral corners of the ocular areas are absent. The bends of the anterior branch of the facial suture are as follows: the ocular bend is weak, the marginal bend is rounded, and the anterior bend is distinct. The cranidium has a broad lingula. The distance between the facial

sutures at the level of the marginal bends is considerably less than at the level of the eye socles. The maximum width of the anterior part of the fixed gena is situated near the eye base. The dorsal furrows are of medium depth in the frontal lobe and small in the basal lobes. The glabellar furrows are absent. The pseudodorsal furrows are of medium depth. The occipital furrow is deep. The fossulae are clear. The paradoublural furrows are weak. The occipital node is distinct. The librigenae are flat. The genal corners are acuminate. The vincular pits are not expressed on the outer surface. The occipital ring and the rings of the body rachis are convex. The pygidium is elongated (mean L/D, 0.62), with rounded lateral margins and a rounded or weakly acuminate posterior end. The rachis is coarsely segmented (four anterior segments are visible, the following segments are either absent or very weakly expressed) and abruptly bordered posteriorly. The pleurae are flat and smooth and are weakly bordered behind the rachis. Closely spaced and numerous D-folds are present on the frontal lobe of the glabella, anterior parts of the fixed genae, the entire surface of the librigenae, and the eye pedicles; widely spaced and coarse folds are present on the rings of the body rachis; these folds emphasize segmentation on the pygidial rachis; they are transverse on the pygidial pleurae and absent from the medial and basal lobes of the glabella and from the occipital ring. The panderian organs are neoasaphine.

**Variability.** The elongation of the pygidium and the acuteness of its posterior margin vary (Pl. 13, figs. 3, 4). The ontogenetic variability shows itself in the size of the eye pedicles, which are very small in juvenile specimens.

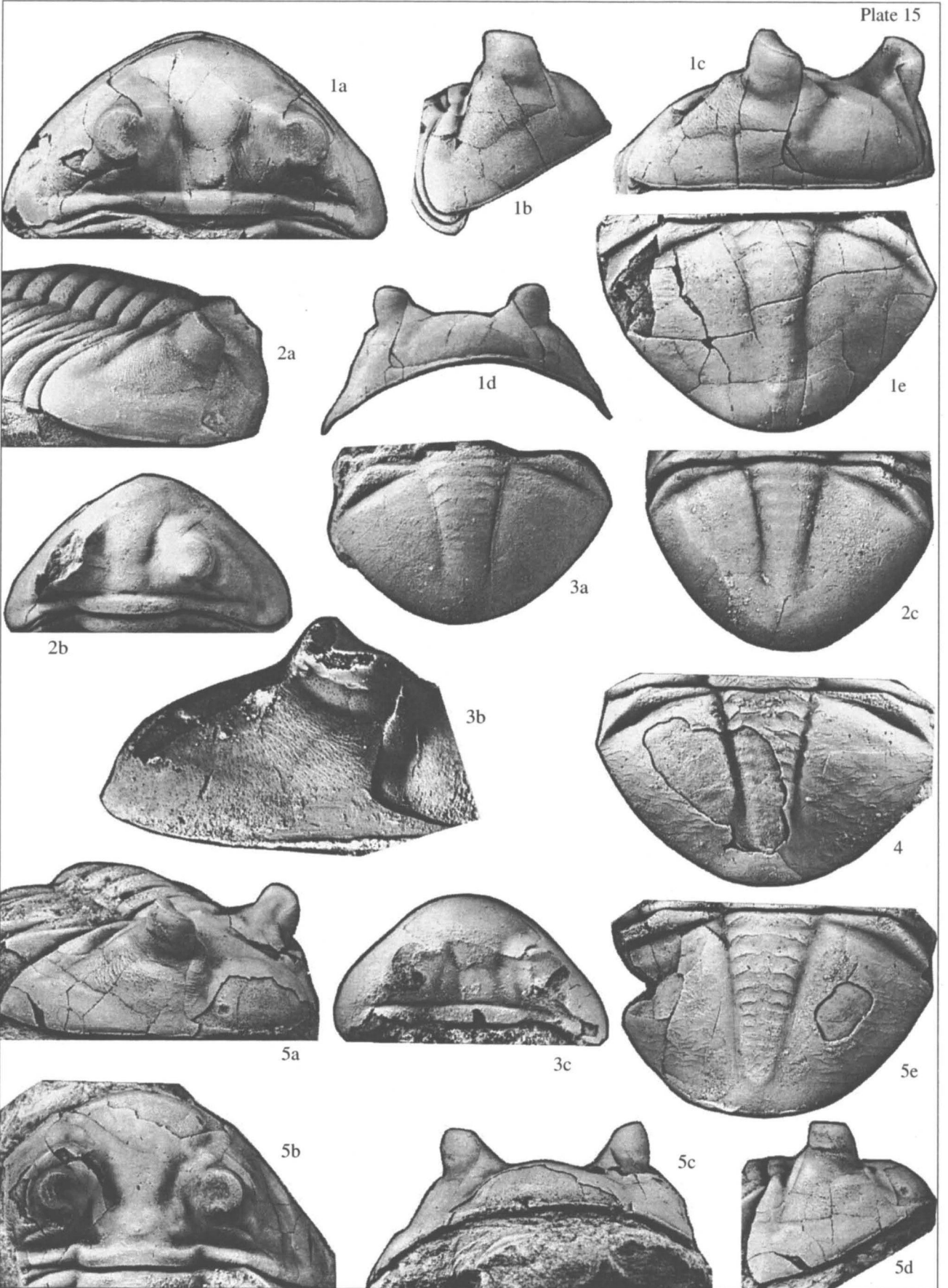
**Comparison.** The most distinctive feature of this species is extremely well-developed eye pedicles, which are well-expressed even in the smallest known (19 mm long including the cephalon) specimens. Other characters are compared in the respective sections dealing with *A. intermedius*, *A. holmi*, *A. plautini*, and *A. latus*.

**Remarks.** The designations of the specimen figured by Schmidt (1901, pl. 2, fig. 11) as the lectotype and holotype by Balashova (1953, 1976) are invalid, since there is no reason to regard it as Lawrow's original specimen.

#### Explanation of Plate 14

**Figs. 1–4.** *Asaphus plautini polyxenus* subsp. nov.: (1) specimen PIN, no. 4330/116, rolled, partially destroyed carapace,  $\times 1.5$ : (1a) dorsal view, (1b) frontal view, (1c) half-turned view, (1d) side view, (1e) pygidium; Volkhov River, Volkhov power station dam outcrop; Aseri Horizon, Duboviki Formation, talus; (2) specimen PIN, no. 4330/118, side view of the cephalon,  $\times 2.1$ ; same locality, Hecker's bed q; collected by Lesnikova; (3) holotype PIN, no. 4330/59, rolled, partially destroyed carapace: (3a) cephalon half-turned view,  $\times 1.5$ ; (3b) pygidium,  $\times 1$ ; left bank of the Volkhov River, near the railroad bridge in the town of Volkhov; Aseri Horizon, Duboviki Formation, the beds with *A. intermedius*–*A. kowalewskii*, 6.5 m above ds4; (4) specimen PIN, no. 4330/117, pygidium,  $\times 1.5$ ; the Ladoga Glint, locality unknown; collected by Balashova.

**Figs. 5–7.** *Asaphus plautini plautini* F. Schmidt, 1901: (5) specimen PIN, no. 4330/54, cephalon compressed longitudinally,  $\times 1$ : (5a) dorsal view, (5b) half-turned view, (5c) frontal view; Volkhov River, Volkhov power station dam outcrop; Aseri Horizon, Duboviki Formation, the beds with *A. intermedius*–*A. kowalewskii*, talus; (6) specimen PIN, no. 4330/121, cephalon with partially destroyed carapace,  $\times 1.5$ : (6a) dorsal view, (6b) frontal view, (6c) side view, (6d) half-turned view; the Ladoga Glint, locality unknown; collected by Balashova; (7) specimen PIN, no. 4330/120, pygidium,  $\times 1$ ; the Ladoga Glint, locality unknown; collected by Balashova.



**Occurrence.** Middle Ordovician, Llanvirn, Aseri Horizon, upper part of the *intermedius-kowalewskii* Beds; upper half of the Duboviki Formation. Outside the Ladoga Glint: Baltic Glint, Leningrad Region, upper part of the Duboviki (?) Formation; Estonia, Aseri Formation (Balashova, 1953, 1976; Rõõmusoks, 1960); Moscow Syncline, Valdai Monocline, Polmet' Formation (Alikhova, 1960; Dmitrovskaya, 1991); northeastern Poland, Białowieża Region, Pomorze Beds (Bednarczyk, 1966).

**Material.** Seventy-two specimens: Volkhov River, 5.3–8.25 m above ds4 or 0.6–3.55 m below the floor of the Porogi Formation; Lava River, 5.8–7.3 m above ds4 or 1.3–2.8 m below the floor of the Porogi Formation.

*Asaphus cornutus* Pander, 1830

Plate 15, figs. 1–3

*Asaphus cornutus*: Pander, 1830, p. 137; Schmidt, 1901, p. 47 (part), pl. 4, figs. 4 and 7 (?) (non pl. 4, fig. 1 = *A. kotlukovi* Balashova; pl. 4, figs. 2 and 3, pl. 12, fig. 11, text-fig. 35 = *A. holmi* F. Schmidt; pl. 4, fig. 5 = *A. punctatus* Lesnikova).

*Asaphus (Trematophorus) cornutus*: Balashova, 1953, p. 405, pl. 1, fig. 10 (?) (non pl. 4, figs. 17–19 = *A. holmi* F. Schmidt).

*Asaphus (Neoasaphus) cornutus*: Jaanusson, 1953a, p. 398; Balashova, 1976, p. 17.

**Neotype.** GMAGI, no. 38/11152, unrolled carapace, figured by Schmidt (1901, pl. 4, fig. 4), designated here; Chudleigh; substage C<sub>1a</sub>; collected by Folbort.

**Diagnosis.** Cephalon of medium proportions, without beaklike bend, glabella reaching anterior margin; basal lobes lenslike; rudiments of glabellar lobes absent; occipital furrow deep; paradoublural furrows faint; cranidium acuminate anteriorly; marginal bend of anterior branch of facial suture sharply angular; eyes elongated, of medium height, located more than their length from posterior margin; eye pedicles absent; eye lists present; ocular areas elevated above cephalon, with tubercles; occipital ring convex; pygidium of medium proportions, with straightened lateral margins and rounded or slightly acuminate posterior end; rachis faintly subdivided; terracelike folds on anterior part of frontal lobe and on librigenae present.

**Description.** The carapace is of medium size, the maximum measured width of the cephalon is 45 mm; mean d, 30 mm. The cephalon is of medium proportions (mean l/d, 0.48), anteriorly acuminate, without beaklike bend. The frontal lobe is convex, with the maximum convexity in the middle part, reaching the anterior margin, bounded in front by a poorly defined furrow, and bears the longitudinal ridge. The medial lobe is clearly bordered laterally, the flexure between it and the frontal lobe is weak. The basal lobes are lenslike and weakly defined. Rudiments of the glabellar lobes are absent. The eyes are elongated, of medium height, located at a distance somewhat greater than their length from the posterior margin and widely separated (mean lo/l, 0.34; mean ho/lo, 0.79; mean la/lp, 1.4; and mean do/d, 0.58). The eye socles are fully developed. The ocular areas are strongly convex. The eye lists are weakly defined. The tubercles in the posterolateral corners of the ocular areas are distinct. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is sharp and angular, and the anterior bend is poorly defined. The cranidium is acuminate anteriorly. The distance between the facial sutures at the level of the marginal bends is greater than that at the level of the eye socles. The maximum width of the anterior part of the fixed gena is situated on the anterior side of the eye list. The dorsal furrows are weak in the frontal lobe and hardly noticeable in the basal lobes. The glabellar lobes are deep and fused with deep pseudodorsal furrows. The occipital furrow is deep. The fossulae are unclear. The paradoublural furrows are poorly defined. The occipital node is diffused. The librigenae are flat. The genal corners are rounded. The vincular pits are not expressed on the outer surface. The occipital ring is convex. The rings of the body rachis are weakly convex to convex. The pygidium is of medium proportions (mean L/D, 0.59), with a straightened lateral margins and rounded or slightly acuminate posterior end. The rachis is weakly segmented (four or five segments are visible) and weakly bordered posteriorly. The pleurae are flat and smooth and not bordered at the rear of the rachis. The following D-folds are present: weak folds on the anterior margin of the frontal lobe; coarse folds on the anterior margins of the librigenae and on the outer sides of the ocular areas that belong to the librige-

Explanation of Plate 15

**Figs. 1–3.** *Asaphus cornutus* Pander, 1830: (1) specimen PIN, no. 4330/55; unrolled carapace: (1a–1c) cephalon: (1a) dorsal view,  $\times 1.5$ ; (1b) side view,  $\times 1.5$ ; (1c) half-turned view,  $\times 1.5$ ; (1d) frontal view,  $\times 1$ ; and (1e) pygidium,  $\times 1.5$ ; left bank of the Lava River, about 100 m below the Kavra River mouth; Aseri Horizon, Duboviki Formation, *kotlukovi-punctatus* Zone, talus; (2) specimen PIN, no. 4330/100, unrolled, partially destroyed and deformed carapace: (2a, 2b) cephalon: (2a) half-turned view,  $\times 1.5$ ; (2b) dorsal view,  $\times 1.3$ ; (2c) pygidium,  $\times 1.5$ ; left bank of the Volkhov River, village of Zvanka; collected by I. Knyrko in 1900; (3) specimen PIN, no. 4330/103, unrolled, partially destroyed carapace: (3a) pygidium,  $\times 2.5$ ; (3b) gena,  $\times 4$ ; (3c) cephalon, dorsal view,  $\times 2$ ; Volkhov River, Volkhov power station dam outcrop; Aseri Horizon, Duboviki Formation, *kotlukovi-punctatus* Zone, talus.

**Figs. 4 and 5.** *Asaphus holmi* F. Schmidt, 1901: (4) specimen PIN, no. 4330/153, pygidium,  $\times 1.5$ ; Volkhov River, Volkhov town; Aseri Horizon, Duboviki Formation, beds with *A. intermedius*–*A. kowalewskii*, M. Legeev's collection; (5) neotype PIN, no. 4330/60, unrolled, partially destroyed carapace,  $\times 1.5$ : (5a–5d) cephalon: (5a) half-turned view, (5b) dorsal view, (5c) frontal view, (5d) side view, (5e) pygidium; left bank of the Volkhov River, new bridge for motor traffic in the town of Volkhov; Aseri Horizon, upper part of the Duboviki Formation, the beds with *A. intermedius*–*A. kowalewskii*, 6.05 m above ds4.

nae; weak folds emphasizing segmentation on the pygidial rachis; weak, transverse folds on the pleurae; they are absent from the anterior part of the fixed genae, occipital ring, and the rings of the body rachis. The panderian organs are neosaphine.

**Variability.** Juvenile specimens possibly belonging to this species have a more convex frontal lobe of the glabella, deeper dorsal furrows, slightly concave posterior parts of the librigenae, and more pronounced tubercles in the posterolateral corners of the ocular areas (Pl. 15, fig. 3).

**Comparison.** This species is similar to *A. latus* and *A. holmi* in the glabella reaching the anterior margin, acuminate cranidium, in the presence of the paradoublural furrow, convex occipital ring, pygidium having straightened lateral margins, and in the coarse terracelike folds on the librigenae; it differs from *A. holmi* in the deeper occipital furrow, rounded or acuminate posterior end of the pygidium, and less segmented pygidial rachis, and in the less developed terracelike folds on the cephalon; from *A. latus*, it differs in the longer cephalon, eyes being higher and more distant from the posterior margin of the cephalon, presence of the eye lists and tubercles in the posterolateral corners of the ocular areas, swollen ocular areas, angular marginal bend of the anterior branch of the facial suture, deep occipital furrow, absence of the flexure from the pygidium behind the rachis, and in the rounded or acuminate posterior end of the pygidium. This species is similar to *A. plautini* (*A. plautini polyxenus*) in having a cephalon of medium proportions, eyes of medium height, cranidium lacking a lingula, presence of the paradoublural furrow, and in the weakly segmented pygidial rachis; it differs in the swollen ocular areas having distinct tubercles behind the eyes, angular marginal bend of the anterior branch of the facial suture, deep occipital furrow, more convex occipital ring, straightened lateral margins of the pygidium, and in the stronger developed terracelike folds on the genae. The comparison with *A. kotlukovi* is given under the description of the latter species. Juvenile specimens of *A. cornutus* closely resemble *A. punctatus* but differ in the strongly convex ocular areas, lower eyes, and in the presence of the terracelike folds on the librigenae.

**Remarks.** The originals of this species are absent from Pander's collections stored at the StPSMI. Apparently, these are not specimens figured by Schmidt (1901). Hence, designating them as "holotype, F. Schmidt, 1898 (?—Balashova's mistake), pl. 4, fig. 4" and "lectotype, F. Schmidt, 1901, pl. 4, fig. 5" (Balashova, 1953) is not correct. The specimen DPStPSU, no. 591/9243, proposed by Balashova (1953, pl. 4, figs. 17–19) as the neotype (the cited number does not correspond to the specimen's label), belongs to *A. holmi*. See also *Remarks* under the description of *A. kotlukovi tumidus*.

**Occurrence.** Middle Ordovician, Llanvirn, Aseri Horizon, *kotlukovi*–*punctatus* Zone; lower part of the Duboviki Formation. Outside the Ladoga Glint:

Baltic Glint, middle part of the Duboviki Formation, and the Aseri Formation.

**Material.** Thirty-five specimens: Volkhov River, 2.6–3.25 m above ds4 or 5.6–6.25 m below the floor of the Porogi Formation; Lava River, 3 m above ds4 or 5.6 m below the floor of the Porogi Formation.

*Asaphus holmi* F. Schmidt, 1901

Plate 15, figs. 4 and 5

*Asaphus cornutus* var. *holmi*: Schmidt, 1901, pp. 50–52, pl. 4, figs. 8a and 8b.

*Asaphus cornutus*: Schmidt, 1901, pl. 4, figs. 2 and 3, pl. 12, fig. 11, text-fig. 35.

*Asaphus (Trematophorus) holmi*: Balashova, 1953, p. 406.

*Asaphus (Trematophorus) cornutus*: Balashova, 1953, pl. 4, figs. 17–19.

*Asaphus (Trematophorus) latus*: Balashova, 1953, pl. 5, fig. 11.

*Asaphus (Neosaphus) cornutus* var. *holmi*: Jaanusson, 1953a, p. 398.

*Asaphus (Neosaphus) holmi*: Balashova, 1976, p. 17.

**Neotype.** PIN, no. 4330/60, unrolled, partially destroyed carapace, designated here; left bank of the Volkhov River, new bridge for motor traffic in the town of Volkhov; Aseri Horizon, upper part of the Duboviki Formation, 6.05 m above ds4; beds with *A. intermedius*–*A. kowalewskii* (Pl. 15, fig. 5).

**Diagnosis.** Cephalon shortened, without beaklike bend, glabella reaching anterior margin; basal lobes lenslike; rudiments of glabellar lobes absent; occipital furrow shallow, developed along its entire length; paradoublural furrows sharp; cranidium acuminate anteriorly; marginal bend of anterior branch of facial suture sharp; eyes long, moderately high and high, removed about their length from posterior margin; eye pedicles short or absent; eye lists weakly expressed; ocular areas not elevated above cephalon or strongly convex, with tubercles; occipital ring convex; pygidium of medium proportions, with straightened lateral margins and posterior end; rachis coarsely segmented; pleurae segmented on casts; terracelike folds on anterior part of frontal lobe and on librigenae present.

**Description.** The carapace is predominantly large, the maximum measured width of the cephalon is 64 mm; mean d, 46 mm. The cephalon is shortened (mean l/d, 0.45), rounded anteriorly, without beaklike bend. The frontal lobe of the glabella is convex, with the maximum convexity in the anterior part, reaching the anterior margin, weakly bordered anteriorly by a furrow, and bearing a weak longitudinal ridge. The medial lobe is clearly bordered laterally, the flexure between it and the frontal lobe is sharp. The basal lobes are lenslike and weakly defined. Rudiments of the glabellar lobes are absent. The eyes are of medium length and high, situated about their length from the posterior margin of the shield and closely spaced (mean lo/l, 0.28; mean ho/lo, 0.93; mean la/lp, 1.4; and mean do/d, 0.5). The eye socles are fully developed. The eye pedicles are small (if present) or absent. The ocular areas

are either not elevated above the cephalon or strongly convex. The eye lists are weakly expressed. The tubercles in the posterolateral corners of the ocular areas are moderately expressed. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is sharp, and the anterior bend is poorly defined. The cranidium is acuminate anteriorly. The distance between the facial sutures at the level of the marginal bends is greater than that at the level of the eye socles. The anterior part of the fixed gena is approximately uniform in width. The dorsal furrows are deep on the frontal lobe and shallow on the basal lobes. The glabellar furrows are deep and fused with the medium-deep pseudodorsal furrows. The occipital furrow is shallow and well-developed along its entire length. The fossulae are clear. The paradoublural furrows are sharp. The occipital node is distinct. The librigenae are weakly concave in the posterior margin. The genal corners are acuminate. The vincular pits are not expressed on the outer surface. The occipital ring and the rings of the body rachis are convex. The pygidium is of average proportions (mean L/D, 0.59), with straightened lateral and posterior margins. The rachis is coarsely segmented along its entire length (up to 10 or 11 segments are visible) and weakly bordered posteriorly. The pleurae are flat and are not bordered behind the rachis; their outer surfaces are smooth, but their casts bear traces of segmentation. The D-folds are very coarse on the frontal lobe of the glabella, on the anterior parts of the librigenae and fixed genae, on the outer sides of the ocular areas, and on the posterior parts of the librigenae behind the eyes; these folds are rare and coarse on the rings of the body rachis; they emphasize segmentation on the pygidial rachis and are transverse on the pygidial pleurae. The panderian organs are neosaphine.

**Variability.** The development of the eye pedicles, convexity of the glabella, and the ocular areas vary. Thus, for example, Schmidt's specimen (1901, pl. 4, fig. 8) lacks eye pedicles, whereas in private collections, I came across specimens with well-developed eye pedicles, which are equal in height to the eye socle.

**Comparison.** This species is similar to *A. latus* and *A. plautini* in the presence of the paradoublural furrows and the terracelike folds on the librigenae and in the absence of the lingula from the cranidium; it is also similar to the first species in the sharpness of the paradoublural furrows, terracelike folds covering most of the genae, pygidium having its lateral margins straightened and poorly defined segmentation of its pleurae, shortened cephalon, and convex occipital ring; it differs from both forms in the weaker furrows on the cephalon, higher eyes, more distinct tubercles in the posterolateral corners of the ocular areas, sharp marginal bend of the anterior branch of the facial suture, and in the more convex occipital ring; additionally, it differs from *A. latus* in the straightened posterior end of the pygidium, eyes being more distant from the posterior margin of the cephalon, and coarsely segmented pygidial rachis; and from *A. plautini*, in the shorter cephalon and

pygidium, considerably stronger developed terracelike folds in the librigenae, pygidium having its lateral margins straightened and its rachis coarsely segmented, and in the more convex occipital ring. The species under consideration is similar to another species found in association, *A. kowalewskii*, in the numerous and closely spaced terracelike folds on the cephalon and convex occipital ring, but differs in the considerably less developed eye pedicles, presence of tubercles in the posterolateral corners of the ocular areas, and in the pygidium having a stronger segmented rachis and straightened lateral and posterior margins. See the respective sections dealing with *A. lepidurus*, *A. cornutus*, *A. kotlukovi*, and *A. bottnicus* for comparisons with them.

**Remarks.** The only specimen of *Asaphus cornutus* var. *holmi*, which was depicted by Schmidt, is lost. Reexamination of the surviving part of the collection disclosed two more specimens of this species identified by Schmidt as *Asaphus cornutus*: specimen PIN, no. 4248/893 (Schmidt, 1901, pl. 4, fig. 3, text-fig. 35) and specimen GMAGI, no. 40/11152 (Schmidt, 1901, pl. 4, fig. 2–2a, pl. 12, fig. 11<sup>1</sup>). To the same species belongs specimen DPStPSU, no. 673/9243, which is the neotype of *Asaphus (Trematophorus) latus* designated by Balashova (1953, pl. 5, fig. 11) and specimen DPStPSU, no. 591/9243, which is the neotype of *Asaphus (Trematophorus) cornutus* (Balashova, 1953, pl. 4, figs. 17–19). The specimens referred by me to the species *A. holmi*, strikingly differ from each other in eye height, development of the dorsal furrows, and convexity of the frontal lobe of the glabella and the ocular areas; however, fragmentary material and the absence of stratigraphic assignment in the majority of cases prevent defining the taxonomical importance of these variations.

**Occurrence.** Middle Ordovician, Llanvirn, Aseri Horizon, beds with *A. intermedius*–*A. kowalewskii*; upper half of the Duboviki Formation. Outside the Ladoga Glint: Baltic Glint, Leningrad Region, upper part of the Duboviki Formation; Estonia, Aseri Formation (Balashova, 1953, 1976).

**Material.** Sixteen specimens: Volkhov River, 6.15–8.15 m above ds4 or 0.7–2.7 m below the floor of the Porogi Formation; Lava River, 6.85 m above ds4 or 1.75 m below the floor of the Porogi Formation.

#### *Asaphus plautini* F. Schmidt, 1901

Plate 14, figs. 1–7

*Asaphus latus* var. *plautini*: Schmidt, 1901, p. 64, pl. 6, figs. 1 and 2 (non fig. 3 = *A. latus* Pander?), text-fig. 37.

*Asaphus latus*: Schmidt, 1901, fig. 36; Lesnikova and Weber, 1949, p. 287, pl. 70, figs. 4 and 5.

*Asaphus (Trematophorus) plautini*: Balashova, 1953, p. 415, pl. 1, figs. 13, 17, and 34; pl. 2, fig. 15.

*Asaphus (Neosaphus) latus* var. *plautini*: Jaanusson, 1953a, p. 398.

*Asaphus (Neosaphus) plautini*: Balashova, 1976, p. 17.

<sup>1</sup> Not pl. 12, fig. 12 as in Schmidt's paper.

**Neotype.** GMAGI, no. 63/11152, unrolled carapace, figured by Schmidt (1901, pl. 6, fig. 1), designated here; village of Gostilitsy; substage C<sub>1a</sub>.

**Diagnosis.** Cephalon of medium proportions, with or without weak beaklike bend; glabella reaching or not reaching anterior margin; basal lobes lenslike; rudiments of glabellar lobes absent; occipital furrow absent or shallow, developed along its entire length; paradoublural furrows faintly defined to sharp; cranidium acuminate anteriorly; marginal bend of anterior branch of facial suture rounded; eyes of medium length and medium height or low, located about their length from posterior margin; eye pedicles and eye lists absent; ocular areas not elevated above cephalon, tubercles on them hardly noticeable; occipital ring weakly convex to flat; pygidium elongated, with undivided pleurae, with rounded lateral margins and posterior end, rachis faintly subdivided; terracelike folds present on anterior part of frontal lobe and sometimes present in posterolateral corners of ocular areas.

**Description.** The carapace is of medium size or large, the maximum measured width of the cephalon is 61.8 mm; mean d, 37.5 mm. The cephalon is of medium proportions (mean l/d, 0.47–0.5), anteriorly weakly acuminate to acuminate, with or without a weak beaklike bend. The frontal lobe of the glabella is moderately to weakly convex, with the maximum convexity in the anterior part, not reaching or reaching the anterior margin, bordered anteriorly by a poorly defined furrow or not bordered, occasionally with a weak longitudinal ridge. The medial lobe is bordered by a furrow or not bordered, occasionally with a weak longitudinal ridge. The medial lobe is distinctly bordered laterally in small specimens and is weakly bordered in large specimens, the flexure between it and the frontal lobe is weak. The basal lobes are lenslike and weakly defined. Rudiments of the glabellar lobes are absent. The eyes are of medium length and medium height or low, situated about their length from the posterior margin of the shield, moderately or widely separated (mean lo/l, 0.29–0.32; mean ho/lo, 0.65–0.71; mean la/lp, 1.6–1.7; and mean do/d, 0.53–0.57). The eye socles are underdeveloped. The eye pedicles are absent. The ocular areas are not elevated above the cephalon. The eye lists are absent. The tubercles in the posterolateral corners of the ocular areas are weak to almost not expressed. The bends in the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded, the anterior bend is absent. The cranidium is acuminate anteriorly. The distance between the facial sutures at the level of the marginal bends is much greater than that at the level of the eye socles. The anterior part of the fixed gena is approximately uniform in width. The dorsal furrows are of medium depth in the frontal lobe and shallow in the basal lobes. The glabellar furrows are shallow and of medium depth and are fused with the medium-deep pseudodorsal furrows. The occipital furrow is shallow and varies from being

well-developed along its entire length to almost not expressed. The fossulae are diffused to distinct. The paradoublural furrows are faintly outlined to distinct. The occipital node is diffused. The librigenae are flat. The genal corners are somewhat obtuse. The vincular pits are not expressed on the outer surface. The occipital ring and the rings of the body rachis are weakly convex to flat. The pygidium is elongated (mean L/D, 0.63–0.66), with rounded lateral and posterior margins. The rachis is weakly segmented (two or three segments are visible) and weakly bordered posteriorly. The pleurae are flat and smooth and are not bordered behind the rachis. The D-folds are weak on the anterior part of the frontal lobe of the glabella; coarse or lacking in the posterolateral corners of the ocular areas; weak and emphasizing segmentation on the pygidial rachis; and coarse and transverse on the pygidial pleurae. The panderian organs are neoasaphine.

**Subspecies included.** *A. plautini plautini* F. Schmidt, 1901 and *A. plautini polyxenus* subsp. nov.

**Comparison.** From *A. kowalewskii*, in association with which this species occurs, it differs in the absence of the eye pedicles, a less convex occipital ring, fewer terracelike folds on the outer surface of the cephalon, and in the elongated pygidium. The comparison with *A. lepidurus*, *A. holmi*, *A. cornutus*, and *A. kotlukovi* is given under their description. Medium-sized specimens of *A. plautini* are similar to *A. striatus* in the short cephalon but differ in the lower eyes and in the presence of paradoublural furrows and terracelike folds on the anterior margin of the frontal lobe. It is similar to *A. latus* in the relatively low eyes, unelevated ocular areas, rounded marginal bend of the anterior branch of the facial suture, weakly segmented pygidial rachis, and in the presence of paradoublural furrows and terracelike folds on the librigenae; it differs in the more elongated cephalon and pygidium, eyes that are shorter and more distant from the posterior margin of the cephalon, a shallower occipital furrow, a less convex occipital ring, a pygidium having undivided pleurae and rounded lateral margins and posterior end, and in the poorly developed terracelike folds on the genae.

**Remarks.** Schmidt's specimen (1901, pl. 6, figs. 3, 3a), which was designated by Balashova (1953) as the lectotype of the species, is lost. In Schmidt's paper, this specimen was depicted worse than the others. However, judging from the large eyes and straightened lateral margins of the pygidium, it most likely belongs to *A. latus* Pander. Therefore, I designate here a neotype among the type species (GMAGI, no. 63/11152). The selected specimen has characters of the subspecies *A. plautini plautini*. The invalidity of the neotype designated by Balashova (1953) is discussed in the introductory part of Systematic Paleontology.

**Occurrence.** Baltic–Ladoga Glint; Middle Ordovician, Llanvirn, Aseri Horizon, beds with *A. intermedius*–*A. kowalewskii*.

*Asaphus plautini plautini* F. Schmidt, 1901

Plate 14, figs. 5–7

*Asaphus latus* var. *plautini*: Schmidt, 1901, p. 64, pl. 6, figs. 1 and 2 (non fig. 3 = *A. latus* Pander?).

*Asaphus latus*: Lesnikova and Weber, 1949, p. 287, pl. 70, figs. 4 and 5.

*Asaphus (Trematophorus) plautini*: Balashova, 1953, p. 415, pl. 1, figs. 13 and 17.

*Asaphus (Neosaphus) atus* var. *plautini*: Jaanusson, 1953a, p. 398.

*Asaphus (Neosaphus) plautini*: Balashova, 1976, p. 17.

**Neotype.** The type of the species.

**Diagnosis.** Eyes low; paradoublural furrow sharp; occipital ring flat; terracelike folds on sides of ocular areas absent.

**Comparison.** This species differs from *A. plautini polyxenus* in the lower eyes, sharper paradoublural furrows, flat occipital ring, absence of terracelike folds from the outer sides of the ocular areas, and in the more elongated pygidium.

**Occurrence.** Middle Ordovician, Llanvirn, Aseri Horizon, upper part of the beds with *A. intermedius*–*A. kowalewskii*; upper part of the Duboviki Formation. Outside the Ladoga Glint: Baltic Glint, Leningrad Region, upper part of the Duboviki Formation; Estonia, Aseri Formation (Balashova, 1953, 1976).

**Material.** Thirty-five specimens: Volkhov River, 6.85–7.85 m above ds4 or 1–2 m below the floor of the Porogi Formation; Lava River.

*Asaphus plautini polyxenus* subsp. nov.

Plate 14, figs. 1–4

*Asaphus latus* var. *plautini*: Schmidt, 1901, fig. 37.

*Asaphus latus*: Schmidt, 1901, fig. 36.

*Asaphus (Trematophorus) plautini*: Balashova, 1953, pl. 1, fig. 34; pl. 2, fig. 15.

**Etymology.** From Greek *poly* (many) and *xenos* (guest).

**Holotype.** PIN, no. 4330/59, rolled, partially destroyed carapace; left bank of the Volkhov River near the railroad bridge in the town of Volkhov; Aseri Horizon, Duboviki Formation, 6.5 m above ds4; beds with *A. intermedius*–*A. kowalewskii* (pl. 14, fig. 3).

**Diagnosis.** Eyes of medium height; paradoublural furrow weak; occipital ring weakly convex; terracelike folds in posterolateral corners of ocular areas present.

**Comparison.** The comparison with *A. plautini plautini* is given under the description of the latter species.

**Occurrence.** Middle Ordovician, Llanvirn, Aseri Horizon, lower part of beds with *A. intermedius*–*A. kowalewskii*; upper half of the Duboviki Formation. Outside the Ladoga Glint: Baltic Glint, upper half of the Duboviki Formation.

**Material.** Forty-four specimens: Volkhov River, 5.55–6.95 m above ds4 or 1.9–3.3 m below the floor of the Porogi Formation; Lava River.

*Asaphus latus* Pander, 1830

Plate 16, figs. 4–9

*Asaphus latus*: Pander, 1830, p. 136; Schmidt, 1901, p. 62, pl. 6, figs. 4, 5, text-fig. 10 (non text-fig. 36 = *A. plautini polyxenus*).

*Asaphus latus* var. *plautini*: Schmidt, 1901, pl. 6, fig. 37.

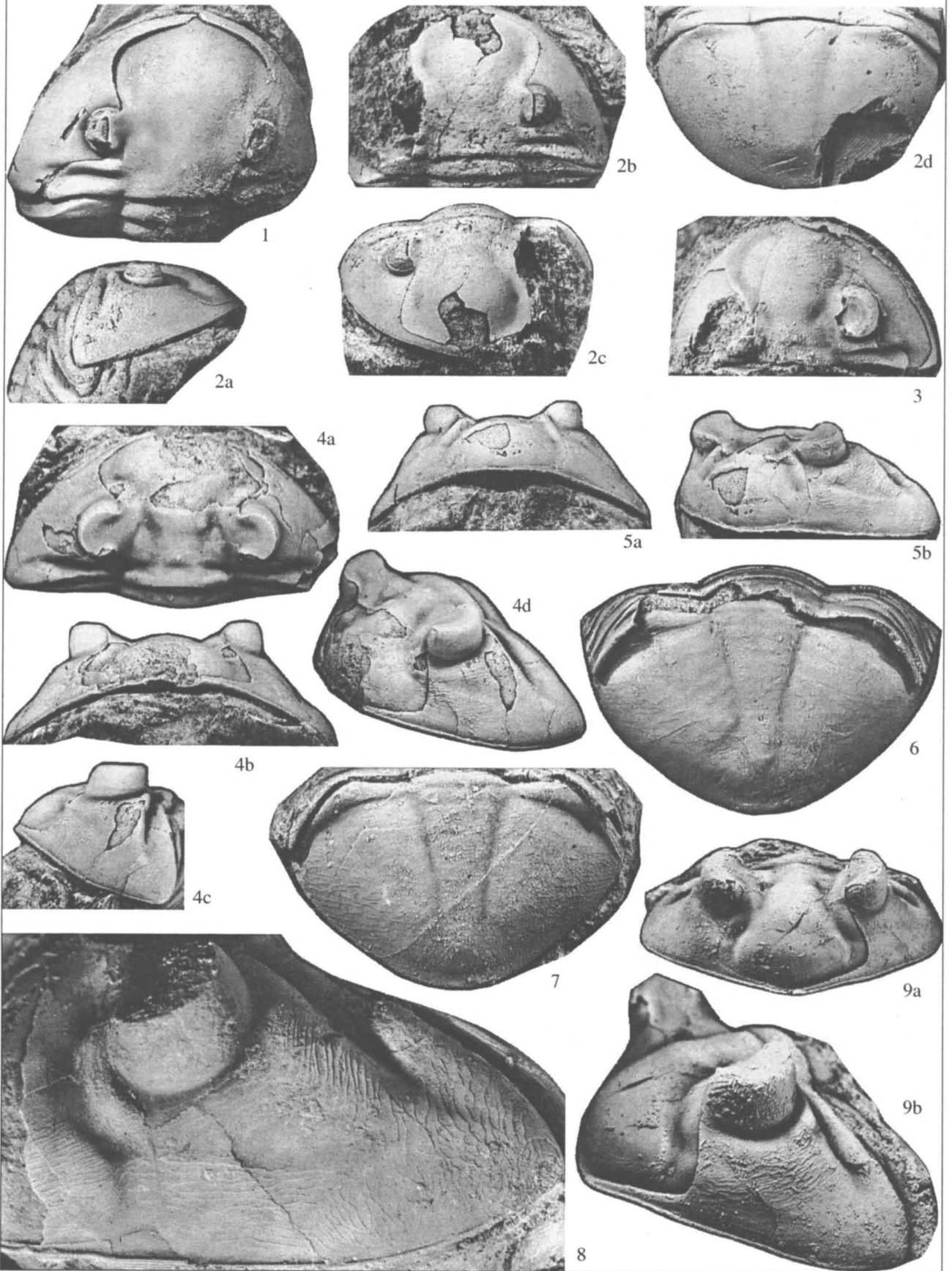
*Asaphus (Trematophorus) latus*: Balashova, 1953, p. 413, pl. 1, figs. 24 and 36 (?) (non pl. 5, fig. 11 = *A. holmi*).

*Asaphus (Neoasaphus) latus*: Jaanusson, 1953a, p. 398; Balashova, 1976, p. 17.

**Neotype.** PIN, no. 4330/112, partially destroyed carapace, designated here; left bank of the Volkhov River, near the railroad bridge in the town of Volkhov; Aseri Horizon, Duboviki Formation, beds with *A. intermedius*–*A. kowalewskii* (pl. 16, fig. 4).

**Diagnosis.** Cephalon shortened, without beaklike bend; glabella reaching anterior margin; basal lobes lenslike; rudiments of glabellar lobes absent; occipital furrow of medium depth; paradoublural furrows sharp; cranium acuminate anteriorly; marginal bend of anterior branch of facial suture rounded; eyes long and low and located about half of their length from posterior margin; eye pedicles and eye lists absent; ocular areas not elevated above cephalon and devoid of tubercles; occipital ring convex; pygidium of medium proportions with straightened lateral margins and acuminate posterior end; rachis faintly subdivided; pleurae weakly segmented and bordered behind rachis; terracelike folds on anterior part of frontal lobe and on librigenae present.

**Description.** The carapace is of medium size and large, the maximum measured width of the cephalon is 54 mm; mean d, 40.5 mm. The cephalon is shortened (mean l/d, 0.42), weakly acuminate anteriorly, without a beaklike bend. The frontal lobe of the glabella is moderately convex, with the maximum convexity in the anterior part, reaching the anterior margin, weakly bordered anteriorly by a furrow, and bearing a weak longitudinal ridge. The medial lobe is clearly bordered laterally, the flexure between it and the frontal lobe is weak or absent. The basal lobes are lenslike and weakly defined. Rudiments of the glabellar lobes are absent. The eyes are long and low, situated half of their length from the posterior margin of the shield, and moderately spaced (mean lo/l, 0.34; mean ho/lo, 0.65; mean la/lp, 1.8; and mean do/d, 0.56). The eye socles are underdeveloped. The eye pedicles, eye lists, and tubercles in the posterolateral corners of the ocular areas are absent. The ocular areas are not elevated above the cephalon. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded, the anterior bend is absent. The cranium is acuminate anteriorly. The distance between the facial sutures at the level of the marginal bends is greater than that at the level of the eye socles. The anterior part of the fixed gena is approximately uniform in width. The dorsal furrows are of medium depth in the frontal lobe and shallow in the basal lobes. The glabellar lobes are deep and fused with medium-deep pseudodorsal furrows. The occipital furrow is of medium depth and is



well-developed along its entire length. The fossulae are clear. The paradoublural furrows are distinct. The occipital node is diffused. The librigenae are flat. The genal corners are rounded to acuminate. The vincular pits are not expressed on the outer surface. The occipital ring is convex. The rings of the body rachis are moderately convex to flat. The pygidium is of medium proportions (mean L/D, 0.57), with straightened lateral margins, and acuminate posteriorly. The rachis is weakly segmented (two or three indistinct segments are present) and weakly bordered posteriorly. The pleurae are flat, with segmentation on the rachial sides, traces of which are poorly defined on the outer surface but distinct on the casts and are bordered at the rear of the rachis. The D-folds are coarse, cover the anterior part of the frontal lobe of the glabella, the anterior parts of the fixed genae, and the entire surface of the librigenae, except for the areas surrounding the paradoublural furrows; on the pygidial rachis, these folds emphasize segmentation and are transverse on the pygidial pleurae; they are absent from the occipital part of the glabella, occipital ring, and rings of the body rachis. The pandurian organs are neosaphine.

See the respective sections dealing with *A. pachyphthalmus*, *A. cornutus*, *A. holmi*, and *A. plautini* for comparisons with them. This species and *A. kowalewskii*, which occurs in association with it, are similar in the shortened cephalon, lower ocular areas, absence of tubercles behind the eyes, pygidium tapering posteriorly and being bordered behind the rachis, and the wide distribution of the terracelike folds over the genae; this species differs in the low and long eyes without eye pedicles, pygidium having its lateral margins straightened, and the pleurae being segmented.

**Remarks.** The specimens depicted by Schmidt (1901, pl. 6, fig. 4) and designated as the holotype (Balashova, 1976) or lectotype (Balashova, 1953) of the species is, in fact, a neotype, since it does not belong to Pander's originals. That specimen, like all other specimens of the type series, is lost. The specimen DPS/PSU, no. 673/9243, proposed by Balashova

(1953, pl. 5, fig. 11) as a neotype (the number in her paper differs from that in the specimen's label) belongs to *A. holmi*. Thus, a neotype selected in the PIN collection is designated in the present work.

**Occurrence.** Middle Ordovician, Llanvirn, Aseri Horizon, beds with *A. intermedius*–*A. kowalewskii*; upper half of the Duboviki Formation. Outside the Ladoga Glint: Baltic Glint, upper half of the Duboviki Formation, Aseri Formation.

**Material.** Seventy-eight specimens: Volkhov River, 5.25–6.85 m above ds4 or 2–3.6 m below the floor of the Porogi Formation; Lava River.

#### *Asaphus bottnicus* Jaanusson, 1953

Plate 17, figs. 1–3

*Asaphus ornatus*: Schmidt, 1901, p. 68, pl. 6, figs. 7–12; pl. 12, figs. 25 and 26; text-figs. 38–40, and 42 (non pl. 6, fig. 6, text-fig. 41 = *Asaphus* (?) *ornatus* Pompecki, 1890); Lesnikova and Weber, 1949, p. 286, pl. 71, fig. 1.

*Asaphus (Trematophorus) ornatus*: Balashova, 1953, p. 416, pl. 1, figs. 8 and 15; pl. 2, figs. 8 and 9.

*Asaphus (Neosaphus) bottnicus*: Jaanusson, 1953b, p. 484, pl. 6, figs. 2–7. *Asaphus (Neosaphus) ornatus*: Balashova, 1976, p. 18.

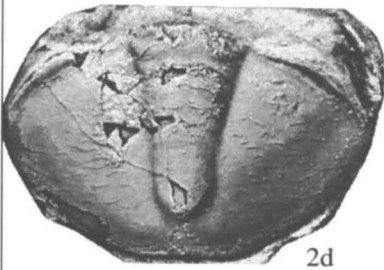
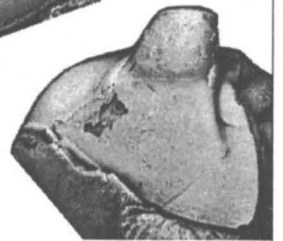
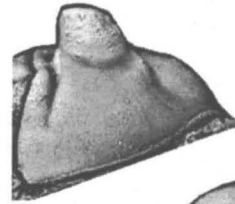
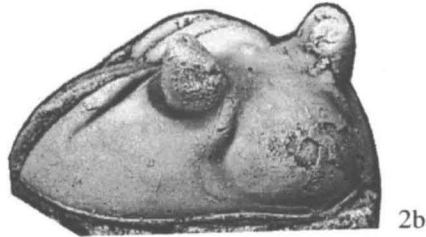
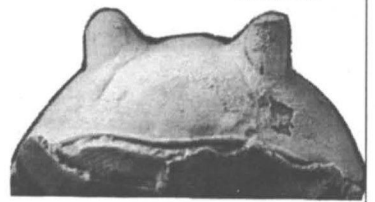
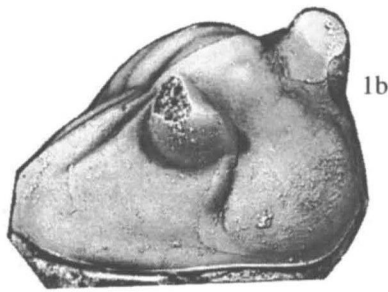
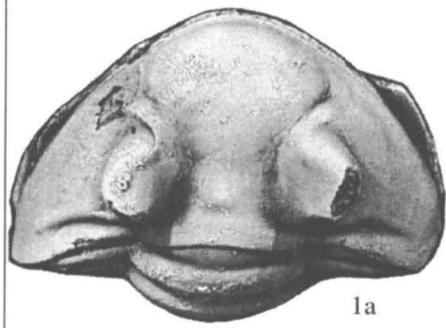
**Holotype.** PIUU, no. 4134, unrolled carapace, designated by Jaanusson (1953b, pl. 6, figs. 2–4); Sweden, Lake Erken; stratigraphic position unknown.

**Diagnosis.** Cephalon of medium proportions, with a hardly noticeable beaklike bend; glabella reaching anterior margin; basal lobes lenslike; rudiments of glabellar lobes absent; occipital and paradoublural furrows absent; cranidium with broad and short lingula, marginal bend of anterior branch of facial suture rounded; eyes long, of medium height, located less than half of their length from posterior margin; eye pedicles and eye lists absent; ocular areas not elevated above cephalon and devoid of tubercles; occipital ring flat; pygidium of medium proportions, with rounded or straightened lateral margins and somewhat obtuse posterior end; rachis coarsely segmented; pleurae sometimes segmented; terracelike folds present on anterior part of frontal lobe and, occasionally, on librigenae.

#### Explanation of Plate 16

**Figs. 1–3.** *Asaphus? broeggeri* F. Schmidt, 1901: (1) specimen PIN, no. 4330/9, partially deformed cephalon,  $\times 1.5$ ; Volkhov River, Babino outcrop; Volkhov Horizon, Volkhov Formation, Zheltyaki Member, beds with *A. ? broeggeri*, 0.65 m above the floor of the member; (2) specimen PIN, no. 4330/8, unrolled, partially destroyed carapace,  $\times 1.5$ : (2a–2c) cephalon: (2a) lateral view, (2b) dorsal view, (2c) view from the frontal lobe, (2d) pygidium; Volkhov River; Volkhov Formation, Zheltyaki Member; collected by Lesnikova; (3) specimen PIN, no. 4330/65, cephalon of a small individual,  $\times 2.5$ ; Putilovo outcrop; Volkhov Horizon, Volkhov Formation, Zheltyaki Member, the beds with *A. ? broeggeri*, 1.05–1.15 m above the floor of the member.

**Figs. 4–9.** *Asaphus latus* Pander, 1830: (4) neotype PIN, no. 4330/112, cephalon,  $\times 1.5$ : (4a) dorsal view, (4b) frontal view, (4c) side view, (4d) half-turned view; left bank of the Volkhov River, Volkhov town, near the railroad bridge; Aseri Horizon, Duboviki Formation; beds with *A. intermedius*–*A. kowalewskii*; (5) specimen PIN, no. 4330/53, cephalon,  $\times 1$ : (5a) frontal view, (5b) half-turned view; right bank of the Ruditsy River near the village of Lopukhinka; same stratigraphical position and age, talus; (6) specimen PIN, no. 4330/113, pygidium,  $\times 2$ ; Volkhov River, village of Byl'shchina, stratigraphical position unknown; collected by I. Knyrko in 1898–1902; (7) specimen PIN, no. 4330/114, pygidium,  $\times 2$ ; left bank of the Volkhov River, Volkhov town, near the railroad bridge; Aseri Horizon, Duboviki Formation; the beds with *A. intermedius*–*A. kowalewskii*, 6.65 m above ds4; (8) specimen PIN, no. 4330/157, cephalon half-turned view, terracelike folds of the gena and the anterior slope of the glabella,  $\times 4$ ; Volkhov River; Aseri Horizon, Duboviki Formation; collected by Lesnikova; (9) specimen PIN, no. 4330/102, cephalon of small individual: (9a) view from the frontal lobe,  $\times 2.7$ ; (9b) half-turned view,  $\times 5$ ; Volkhov River, Volkhov power station dam outcrop; Aseri Horizon, Duboviki Formation; the beds with *A. intermedius*–*A. kowalewskii*, talus.



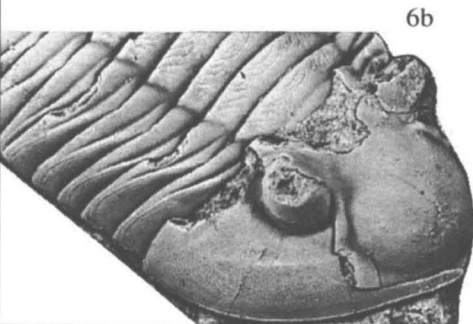
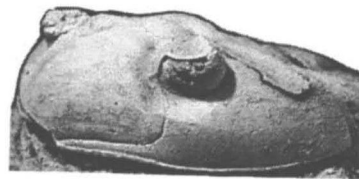
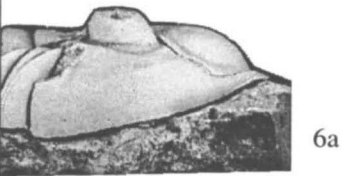
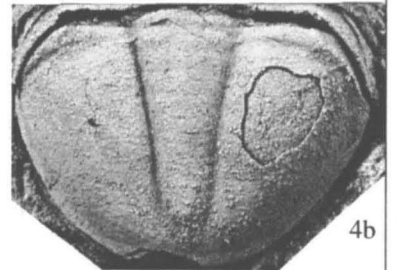
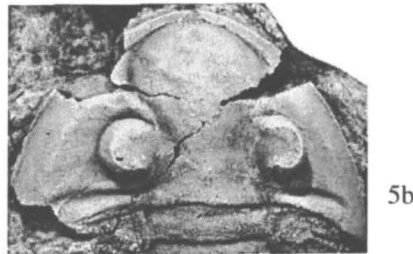
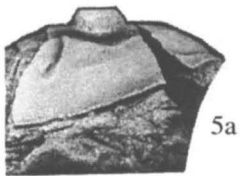
1d

4a

4b

4c

6d



**Description.** The carapace is of medium size or small, the maximum measured width of the cephalon is 32 mm; mean  $d$ , 30 mm. The cephalon is of average proportions (mean  $l/d$ , 0.51), weakly acuminate anteriorly, possessing a hardly noticeable beaklike bend. The frontal lobe of the glabella is strongly convex, with the maximum convexity in the middle part, reaching the anterior margin, weakly bordered anteriorly by a furrow, occasionally having a weak longitudinal ridge. The medial lobe is clearly bordered laterally, the flexure between it and the frontal lobe is weak. The basal lobes are lenslike and almost not expressed on the outer surface of the shield. Rudiments of the glabellar lobes are absent. The eyes are long and high, and are situated slightly less than half of their length from the posterior margin of the shield and moderately spaced (mean  $lo/l$ , 0.36; mean  $ho/lo$ , 0.85; mean  $la/lp$ , 2.6; and mean  $do/d$ , 0.55). The eye socles are fully developed. The eye pedicles, eye lists, and tubercles in the posterolateral corners of the ocular areas are absent. The ocular areas are not elevated above the cephalon. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is sharp and more or less rounded, and the anterior bend is poorly defined. The cranium has a short and wide lingula. The distance between the facial sutures at the level of the marginal bends is greater than that at the level of the eye socles. The anterior part of the librigena is uniform in width. The dorsal furrows are deep on the frontal lobe and absent from the basal lobes. The glabellar and pseudodorsal furrows are fused and shallow. The occipital and paradoublural furrows are absent. The fossulae are diffused to distinct. The occipital node is distinct. The librigenae are flat. The genal corners are acuminate. The vincular pits are not expressed on the outer surface. The occipital ring is flat. The rings of the body rachis are convex. The pygidium is predominantly of medium proportions (mean  $L/D$ , 0.57), with rounded or straightened lateral margins and obtuse posterior end. The rachis is broad, short, coarsely segmented (four or five coarse segments are visible on the carapace surface, they are followed by three or four weakly expressed segments), and clearly bordered posteriorly. The pleurae are flat, with or without traces of segmen-

tation along the rachial margins, and are not bordered behind the rachis. The D-folds are coarse, cover the anterior part of the frontal lobe of the glabella, sometimes they cover the posterior parts of the librigenae behind the marginal furrows, ring of the body rachis, pygidial rachis (emphasize segmentation), pygidial pleurae (radial and transverse folds; occasionally, radial folds disintegrate into a series of transverse folds); these folds are absent from the other areas, including most of the librigenae, occipital glabella, and the occipital ring. The librigena surface is covered with rare coarse pits. The panderian organs are neosaphine.

**Variability.** The material from the Ladoga Glint varies mainly in the convexity of the frontal lobe of the glabella, in shortening of the pygidium, segmentation of the rachis, and in the expression of the terracelike folds on the posterior margins of the librigenae, pleurae, and pygidial rachis.

**Comparison.** Specimens from the Ladoga Glint differ from the Swedish representatives in the more convex frontal lobe of the glabella reaching the anterior margin, in higher eyes, acuminate genal corners, more strongly segmented (in some cases) pygidial rachis, and in the presence of terracelike folds on the anterior part of the frontal lobe. It is similar to *A. ingrianus* and medium-sized *A. kotlukovi* and *A. cornutus* but differs from them in the eyes being closer to the posterior margin, shorter pygidium possessing straightened lateral margins, and in the more coarsely segmented rachis. Additionally, it differs from *A. kotlukovi* and *A. cornutus* in the low ocular areas, absence of tubercles from the posterolateral corners of the ocular areas, and in the absence of the occipital furrow; in addition, it differs from *A. kotlukovi* in the pygidial rachis being stronger bordered posteriorly and from *A. cornutus* in the absence of paradoublural furrows and terracelike folds from the librigenae. This species differs from *A. ingrianus* also in the frontal lobe of the glabella being closer to the anterior margin, in the large eyes, rounded marginal bend of the anterior branch of the facial suture, the presence of the lingula on the cranium, a flat occipital ring, and in the absence of the occipital furrow. From one of the *A. holmi*, which has nonpediculate eyes and weakly developed terracelike folds, it differs in the eyes

#### Explanation of Plate 17

**Figs. 1–3.** *Asaphus bottmicus* Jaanusson, 1953: (1) specimen PIN, no. 4330/125, cephalon of the rolled carapace: (1a) dorsal view,  $\times 2$ ; (1b) half-turned view,  $\times 2$ ; (1c) frontal view,  $\times 1.5$ ; (1d) side view,  $\times 2$ ; Volkhov River, Shkurina Gorka outcrop; Lasnamägi Horizon. Porogi Formation, the beds with *A. bottmicus*, 5.3 m above the floor of the formation; (2) specimen PIN, no. 4330/143, rolled, partially destroyed carapace,  $\times 1.5$ : (2a–2c) cephalon: (2a) dorsal view, (2b) half-turned view, (2c) side view, (2d) pygidium; same age and locality, 5.15 m above the floor of the Porogi Formation; (3) specimen PIN, no. 4330/152, pygidium,  $\times 2$ ; the Ladoga Glint, locality unknown; collected by Balashova.

**Fig. 4.** *Asaphus* sp., specimen PIN, no. 4330/34, unrolled, partially destroyed and deformed carapace,  $\times 1.5$ : (4a) cephalon, (4b) pygidium; Volkhov River, Zvanka outcrop; Kunda Horizon, Obukhovo Formation, Member 3, *raniceps–striatus* Zone, 4.1 m above ds3.

**Figs. 5 and 6.** *Asaphus? ornatus* Pompecki, 1890: (5) specimen PIN, no. 4330/144, incomplete cephalon,  $\times 1.5$ : (5a) lateral view, (5b) dorsal view; Volkhov River, Shkurina Gorka outcrop; Lasnamägi Horizon. Porogi Formation, beds with *A. bottmicus*, 6.4 m above the floor of the Porogi Formation; (6) neotype PIN, no. 4330/127, unrolled carapace with deformed cephalon: (6a) cephalon,  $\times 1.5$ ; (6b) pygidium,  $\times 1.5$ ; (6d) general appearance,  $\times 1$ ; same age and locality, 5.6 m above the floor of the Porogi Formation.

being relatively large and closer to the posterior margins, in the absence of tubercles from the posterolateral corners of the ocular areas, in the absence of the occipital and paradioubrural furrows, terracelike folds from the genae, in the rounded bend of the anterior branch of the facial suture, the presence of the lingula on the cranium, and in the flat occipital ring. The comparison with *A. lepidurus* and *A. ? ornatus* is given under their description.

**Remarks.** Despite these differences between the Swedish and Ladoga specimens, I refer them to a single species, for these differences are of minor importance, whereas their stratigraphic position is roughly the same.

**Occurrence.** Middle Ordovician, Llanvirn, Llanvirn Formation, the beds with *A. bottnicus*; Porogi Formation. Outside the Ladoga Glist: Baltic Glist (Balashova, 1976); Moscow Syncline, Valdai Monocline, Polomet' Formation (Alikhova, 1960; Dmitrovskaya, 1991); Sweden, Lake Siljan Region, Furudal Limestone, Öland Island, Southern Bothnian Region; Norway: Oslo Region (Jaanusson, 1953b; 1963).

**Material.** Thirty specimens: Volkhov River, 5.05–6.3 m above the floor of the formation; Lava River.

*Asaphus* sp.

Plate 17, fig. 4

**Description.** The carapace is of medium size, the cephalon width is 35.8 mm. The cephalon is shortened ( $l/d$ , 0.45), rounded anteriorly, with a weak beaklike bend. The frontal lobe of the glabella is strongly convex, with the maximum convexity in the middle part, reaching the anterior margin, not bordered anteriorly, lacking the longitudinal ridge. The medial lobe is not bordered laterally, the flexure between it and the frontal lobe is absent. The basal lobes are lenslike and distinct. Rudiments of the glabellar lobes are present. The eyes are long, of medium height, located about their length from the posterior margin of the shield ( $lo/l$ , 0.35;  $ho/lo$ , 0.72; and  $la/lp$ , 1.3). The eye sockets are fully developed. The eye pedicles, eye lists, and tubercles in the posterolateral corners of the ocular areas are absent. The ocular areas are not elevated above the cephalon. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded, and the anterior bend is poorly defined. The cranium is weakly acuminate anteriorly. The distance between the facial sutures at the level of the marginal bends is greater than that at the level of the eye sockets. The dorsal furrows are weak in the frontal lobe and absent from the basal lobes. The glabellar furrows are of medium depth and are fused with the weak pseudodorsal furrows. The occipital furrow is shallow and well-developed along its entire length. The paradioubrural furrows are absent. The fossulae are unclear. The occipital node is distinct. The librigenae are convex. The genal corners are acuminate. The vincular pits are not expressed on the outer surface.

The occipital ring and the rings of the body rachis are flat. The pygidium is elongated (mean  $L/D$ , 0.65), with rounded lateral and posterior margins. The rachis is long, weakly segmented (four segments are visible) and abruptly bordered posteriorly. The pleurae are weakly convex and smooth and are not bordered at the rear of the rachis. Both radial and transverse D-folds are present on the entire surface of the frontal lobe of the glabella, on the rings of the body rachis, and on the pygidial pleurae. The ornamentation of the outer surface of the carapace is typical of *Asaphus*. The structure of the panderian organs is unknown.

**Comparison.** This species is similar to *A. pachyophthalmus*, *A. sulevi*, and *A. knyrkoi* in the more or less rounded anteriorly cephalon and the convex frontal lobe of the glabella but differs from *A. pachyophthalmus* in the lower eyes, full absence of the bend of the shield margin over the vincular pits, a longer pygidium, and in the better developed terracelike folds of the glabella; from *A. sulevi*, in the less convex glabella, less developed furrows on the cephalon, flat occipital ring and flat rings of the body rachis, on elongated pygidium possessing a less segmented rachis, and in the more poorly expressed folds of the diagnostic areas; from *A. knyrkoi*, in the longer eyes, more elongated pygidium with a narrower and not low rachis, and in the absence of a coarsely pitted ornamentation from the outer surface of the carapace. It differs from the stratigraphically close *A. striatus* in the shorter and obtuse cephalon, stronger convex frontal lobe, flatter pygidial pleurae, and in the presence of numerous terracelike folds on the frontal lobe of the glabella.

**Occurrence.** Middle Ordovician, Llanvirn, Kunda Horizon, *raniceps-striatus* Zone; Volkhov River, Zvanka outcrop (Fig. 12); Obukhovo Formation, Member 3; 4.1 m above ds3.

**Material.** One specimen.

*Asaphus? broeggeri* F. Schmidt, 1901

Plate 16, figs. 1–3

*Asaphus broeggeri*: Schmidt, 1898, p. 20 (nom. nud.); 1901, p. 21, pl. 2, figs. 4–7; pl. 12, fig. 5; text-figs. 4 and 13; Lamanskii, 1905, p. 62; Lesnikova and Weber, 1949, p. 284, pl. 68, figs. 1 and 2.

*Asaphus (Schizophorus) broeggeri*: Balashova, 1953, p. 388, pl. 1, fig. 1, pl. 2, figs. 1 and 2.

*Asaphus (Asaphus) broeggeri*: Jaanusson, 1953a, p. 397; Balashova, 1976, p. 8.

**Lectotype.** PIN, no. 4248/92, unrolled, partially destroyed carapace, depicted by Schmidt (1901, pl. 2, fig. 4), designated by Balashova (1953); Volkhov River, village of Izvoz; substages B<sub>2a</sub>–b.

**Diagnosis.** Cephalon elongated, acuminate anteriorly, glabella not reaching anterior margin; basal lobes lenslike and almost not expressed on outer surface of carapace; rudiments of glabellar lobes absent; eyes low; weak list present at posterior margin of ocular area; genal corners acuminate and lacking of spines; occipital furrow absent; pygidium of medium propor-

tions, rachis undivided; pleurae unsegmented; D-folds absent; panderian organs asaphine.

**Description.** The carapace is of medium size, the maximum measured width of the cephalon is 41.5 mm; mean  $d$ , 37 mm. The cephalon is elongated (mean  $l/d$ , 0.54), slightly acuminate anteriorly, with a weak beaklike bend. The frontal lobe of the glabella is moderately convex, with the maximum convexity in the middle part, not reaching the anterior margin, weakly bordered anteriorly by a furrow, and bearing a weak longitudinal ridge. The medial lobe is clearly bordered laterally, the flexure between it and the frontal lobe is absent. The basal lobes are lenslike and almost not expressed on the outer surface of the shield but distinct on the casts. Rudiments of the glabellar lobes are absent. The eyes are of medium length and low, situated by approximately their length from the posterior margin of the shield, moderately to widely separated (mean  $lo/l$ , 0.26; mean  $ho/lo$ , 0.66; mean  $la/lp$ , 1.8; and mean  $do/d$ , 0.57). The eye socles are underdeveloped. The eye pedicles, eye lists, and tubercles in the posterolateral corners of the ocular areas are absent. The ocular areas are not elevated above the cephalon, narrow and weakly developed ridges extend along their posterior margins. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is sharp and angular, and the anterior bend is distinct. The cranidium has a narrow lingula. The distance between the facial sutures at the level of the marginal bends is greater than that at the level of the eye socles. The anterior part of the fixed gena is uniform in width or slightly widens near the anterior margin. The dorsal furrows are of medium depth on the frontal lobe and absent from the basal lobes. The glabellar furrows are shallow and are fused with medium-deep pseudo-dorsal furrows. The occipital and paradoublure furrows are absent. The fossulae are absent or diffused. The occipital node is almost absent. The librigenae are weakly convex. The genal corners are acuminate. The vincular pits are small and show themselves on the outer surface only by a faint bend of the lateral margin. The occipital ring and the rings of the body rachis are flat. The pygidium is rounded and of medium proportions (mean  $L/D$ , 0.58). The rachis is of medium width, undivided, and diffused posteriorly. The pleurae are flat and unsegmented and are not bordered behind the rachis. The D-folds are absent; only a series of short fragments of folds is present in the dorsal furrows of the pygidium. The panderian organs are asaphine.

**Variability.** The development of the furrows and the basal lobes varies. A juvenile specimen (Pl. 16, fig. 3) has a shortened and rounded cephalon, a more convex frontal lobe of the glabella, better developed dorsal and glabellar furrows, and longer eyes.

**Comparison.** This species is closest to *A. raniceps*, *A. acuminatus*, and *A. striatus*, to which it is similar in the elongated and acuminate anteriorly cephalon, glabella being more distant from the anterior margin,

lenslike and weakly expressed basal lobes, terracelike folds being not expressed on the outer surface, and the asaphine panderian organs but differs in the basal lobes being almost not visible on the outer surface of the carapace, in the absence of rudimentary lobes, and in the presence of lists on the posterior margin of the ocular areas. The comparison with *A. raniceps* and *A. acuminatus* on the basis of other characters and with the stratigraphically close species *A. lepidurus* is given under their description. The species under consideration is similar to representatives of the family Ptychopygidae in the weakly expressed basal lobes, low eyes, and in the lists on the posterior margins of the ocular areas but differs from them in the absence of genal spines, in the pygidium possessing an unsegmented rachis and pleurae, and in the absence of D-folds.

**Remarks.** The invalidity of the neotype designated by Balashova (1953) is discussed in the introductory part of Systematic Paleontology.

**Occurrence.** Lower Ordovician, Arenig, Volkhov Horizon, beds with *A.?* *broeggeri*; Volkhov Formation, Zheltyaki Member. Outside the Ladoga Glint: Baltic Glint, Toila Formation, Künnapõhja Member; Moscow Syncline, Valdai Monocline, Volkhov Formation (Alikhova, 1960; Dmitrovskaya, 1991); rock masses detached by a glacier in the Tver' Region (Balashova, 1953, 1976).

**Material.** Thirty-seven specimens: Volkhov River, 0.15–0.65 m above the Dikari roof, or 4.3–4.8 m below  $ds_2$ ; Lava River, 0.6–0.95 m above the Dikari roof or 3.75–4.15 m below  $ds_2$ ; village of Putilovo, 1.05–1.2 m above the Dikari roof or 3.65–3.8 m below  $ds_2$ .

*Asaphus?* *ornatus* Pompecki, 1890

Plate 17, figs. 5 and 6

*Asaphus ornatus*: Pompecki, 1890, p. 80, pl. 6, fig. 3; Schmidt, 1901, pl. 6, fig. 6, text-fig. 41.

**Neotype.** PIN, no. 4330/127, unrolled carapace, designated here; Volkhov River, Shkurina Gorka outcrop (Fig. 15); Lasnamägi Horizon, Porogi Formation, 5.6 m above the floor; beds with *A. bottnicus* (Pl. 17, fig. 6).

**Diagnosis.** Cephalon of medium proportions, rounded or slightly acuminate anteriorly; basal lobes lenslike and weakly expressed; glabella far from reaching anterior margin; flexure between frontal and medial lobes sharp; eyes of medium height; located about half of their length from posterior margin of shield; anterior part of fixed gena widening anteriorly; cranidium with medium-wide, long lingula; rings of body rachis flat; pygidium of medium proportions, with straightened posterior end; rachis narrow, long, coarsely segmented, segments not interrupted at its axis; pleurae with weakly expressed segmentation; terracelike folds absent from librigenae.

**Description.** The carapace is of medium size, the cephalon width is 31–37 mm. The cephalon is elon-

gated, acuminate anteriorly, with a weak beaklike bend. The frontal lobe of the glabella is convex, with the maximum convexity in the anterior part, far from reaching the anterior margin, weakly bordered anteriorly by a furrow, and having a weak longitudinal ridge. The medial lobe is weakly bordered laterally, the flexure between it and the frontal lobe is sharp. The basal lobes are lenslike and weakly expressed. Rudiments of the glabellar lobes are absent. The eyes are of medium height, of medium length, and moderately separated, located about half of their length from the posterior margin of the shield. The eye socles are fully developed. The eye pedicles, eye lists, and tubercles in the posterolateral corners of the ocular areas are absent. The ocular areas are not elevated above the cephalon. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded, and the anterior bend is distinct. The cranidium has a medium-wide, long lingula. The distance between the facial sutures at the level of the marginal bends is greater than that at the level of the eye socles. The maximum width of the anterior part of the fixed gena is situated near the anterior margin. The dorsal furrows are deep on the frontal lobe and absent from the basal lobes. The glabellar furrows are shallow and fused with shallow pseudodorsal furrows. The occipital and paradoublural furrows are absent. The fossulae are distinct. The occipital node is poorly defined. The librigenae are weakly convex. The genal corners are acuminate. The vincular pits are small and not expressed on the outer surface. The occipital ring and the rings of the body rachis are flat. The pleural ends are acute and attenuated into short spines. The pygidium is of medium proportions, with rounded lateral margins and a straightened posterior end. The rachis is long, coarsely segmented along its entire length, and abruptly bordered posteriorly. The pleurae are flat, weakly segmented, and not bordered behind the rachis. The D-folds are weak on the frontal lobe of the glabella, coarse on the rings of the body rachis, coarse and emphasizing segmentation on the pygidial rachis, transverse and arranged into radial series along the segments on the pleurae. The librigenae are covered with rare and deep pits. The panderian organs are neosaphine (?).

**C o m p a r i s o n.** On the basis of a number of characters, this species is transitional between the genera *Asaphus* and *Ogmasaphus*. From *Ogmasaphus praetextus* (Törnquist, 1884), it differs in the presence of flexure between the frontal and medial lobes, higher eyes, and in the weaker segmentation of the pygidial pleurae. It resembles *A. bottnicus*, which occurs in association with it and is morphologically similar to it, in the general shape of the cephalon, weakly expressed lenslike basal lobes, eyes being close to the posterior margin, pygidium possessing a straightened posterior margin, coarsely segmented rachis having segments not interrupted at the longitudinal axis and segmented pleurae, and the absence of terracelike folds from the main surface of the librigenae but differs in the frontal lobe

not reaching the anterior margin, narrower and longer lingula of the cranidium, anterior part of the fixed gena widening anteriorly, eyes being lower and more distant from the posterior margin, flat rings of the body rachis, and in the longer pygidium with a longer and narrower rachis and more coarsely segmented pleurae.

**R e m a r k s.** The majority of specimens identified by Schmidt as *Asaphus ornatus* Pompecki (Schmidt, 1901) differ from the figure published by Pompecki (1890, pl. 6, figs. 3–6), only one specimen is similar to this figure (Schmidt, 1901, pl. 6, figs. 6–6a, text-fig. 41). I attribute most specimens of *Asaphus ornatus* from Schmidt's collection, as well as specimens from Balashova's paper (1953, pl. 2, figs. 8, 9), to *A. bottnicus*. Pompecki's collection has not survived and his figures are inadequate to reflect the morphology of the species. For that reason, the neotype is designated here.

**O c c u r r e n c e.** Middle Ordovician, Llanvirn, Llanamägi Horizon, Porogi Formation, beds with *A. bottnicus*. Outside the Ladoga Glint: rock masses detached by a glacier in the southern Baltic Region (Pompecki, 1890).

**M a t e r i a l.** Three carapaces: Volkhov River, 4.8–6.4 m above the floor of the Porogi Formation.

#### **Genus *Subasaphus* Balashova, 1976**

*Asaphus* (*Subasaphus*): Balashova, 1976, p. 11.

*Platyasaphus*: Ivantsov, 2000, p. 52.

**T y p e s p e c i e s.** *Asaphus laevissimus* var. *lati-cauda* Schmidt, 1901.

**D i a g n o s i s.** Cephalon wide, rarely of medium proportions; basal lobes present; eyes low; eye pedicles absent; genal corners with spines, rarely obtuse; vincular apparatus absent from cephalon or represented by weak depressions; pygidium wide; rachis faintly subdivided or smooth, segments interrupted at its axis; cephalon and pygidium not bordered; panderian organs neosaphine and subasaphine.

**D e s c r i p t i o n.** The carapace is of medium size or large, the maximum measured width of the cephalon is 58.5 mm. The cephalon is wide and of medium proportions, weakly acuminate anteriorly, with or, rarely, without a weak beaklike bend. The frontal lobe of the glabella is flat to strongly convex, with the maximum convexity in the middle part, reaching or not reaching the anterior margin, anteriorly bordered by a weak or distinct furrow, and bearing a weak longitudinal ridge. The medial lobe is weakly bordered laterally, the flexure between it and the frontal lobe is weak or absent. The basal lobes are lenslike and weakly defined. Rudiments of the glabellar lobes may be present. The eyes are of medium length, low, located at a distance equal to or slightly greater or less than their length from the posterior margin of the shield, moderately separated or moderately drawn together. The palpebral lobes are situated higher or lower than the middle part of the glabella. The eye socles are underdeveloped. The flexure

between the eye socle and librigena is sharp to weak or absent. The eye pedicles, eye lists, and tubercle in the posterolateral corners of the ocular areas are absent. The ocular areas are not elevated above the cephalon. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded or angular, and the anterior bend is distinct. The cranidium has a broad lingula. The dorsal furrows are distinct on the frontal lobe and weak or absent from the basal lobes. The glabellar furrows are shallow. The pseudodorsal furrows are weakly defined. The occipital furrow is shallow and well-developed along its entire length or absent. The fossulae are clear or poorly defined. The paradiaboulural furrows are absent. The occipital node is distinct or poorly defined. The librigenae are concave in their posterior parts, occasionally with a poorly defined limblike flexure anteriorly. The genal corners are obtuse or have long spines. The vincular pits are not expressed on the outer face. The occipital ring is flat. The rings of the body rachis are flat to weakly convex. The pygidium is wide, with straightened lateral margins and an obtuse posterior end. The rachis is poorly defined, weakly segmented or unsegmented, sharply or faintly bordered posteriorly. The pleurae are flat and smooth and are not bordered behind the rachis. The facets widen toward the lateral corners of the pygidium. The D-folds are present on the anterior part of the frontal lobe of the glabella, on the librigenae near the genal corners and on the spines, and on the anterolateral margins of the pygidial pleurae. The panderian organs are subasaphine and neosaphine.

**Specific composition.** *S. platyurus* (Angelin, 1858), *S. laticaudatus* (F. Schmidt, 1901), *S. latisegmentatus* (Nieszkowskii, 1857), and *S. spinifer* (Ivantsov, 2000).

**Comparison.** This genus differs from the other genera of the subfamily in having the widest cephalon and pygidium, in the presence of genal spines during the last ontogenetic stages in most of the forms, except for the type species.

**Remarks.** The generic name *Platysaphus*, which was earlier proposed by me (Ivantsov, 2000), is invalid because of the priority problem, for the genus includes *A. laticaudatus*, which is the type species of the subgenus *Asaphus* (*Subasaphus*) Balashova (Balashova, 1976). Accordingly, *A. platyurus* Angelin, 1858, proposed by me (Ivantsov, 2000), cannot be the type of this genus, although the main generic characters are developed to the least degree in *A. laticaudatus*.

**Occurrence.** Baltoscandia, probably Novaya Zemlya; Middle Ordovician, Llanvirn, Aseri Horizon. Baltic Glint, Duboviki (?) and Aseri formations (Balashova, 1953, 1976; Rõõmusoks, 1960; Männil, 1963b); Jelgava depression, Baldone Formation, middle part of the Ziemele Member (Ulst *et al.*, 1984); Middle Lithuanian depression, Rokiškis Formation, Vajdlene Member (Lashkov *et al.*, 1984); northwestern slope of the Belarussian Ridge (Alikhova, 1960;

Sverzhinskii *et al.*, 1971); southeastern Latvia (Gailite, 1978; Männil, 1963a; 1966); northeastern Poland (Modlinski and Pokorski, 1964); central Sweden, Lake Siljan Region, Västergötland, Öland Island, Segerstad Limestone (Bohlin, 1949; Jaanusson, 1953b, 1963, 1964). There is evidence that this species has been recorded on Novaya Zemlya, near Guba Loginova Bay (Bondarev, 1960).

***Subasaphus platyurus* (Angelin, 1854)**

*Asaphus platyurus*: Angelin, 1854, p. 54, pl. 30, fig. 1.

*Asaphus* (*Neosaphus*) *platyurus platyurus*: Jaanusson, 1953b, p. 467, pl. 1, figs. 1–6; pl. 2, figs. 1–3, text-figs. 1–3.

**Neotype.** RM, no. 21948, pygidium with a partially destroyed carapace, designated by Jaanusson (1953b); Öland Island; *Platyurus* Limestone.

**Diagnosis.** Eyes are of medium length, removed from the posterior margin at a distance somewhat greater than their length; palpebral lobes are situated below the glabella; flexure between ocular area and librigena is present; occipital furrow absent; panderian organs neosaphine.

**Comparison.** See the respective sections dealing with other species of the genus.

**Occurrence.** Central Sweden, Lake Siljan Region, Västergötland, Öland Island; Middle Ordovician, Llanvirn, Aseri Horizon (Jaanusson, 1953b).

***Subasaphus spinifer* (Ivantsov, 2000)**

Plate 19, figs. 8–10; Plate 21, fig. 13

*Asaphus platyurus*: Lesnikova and Weber, 1949, pl. 69, fig. 4.

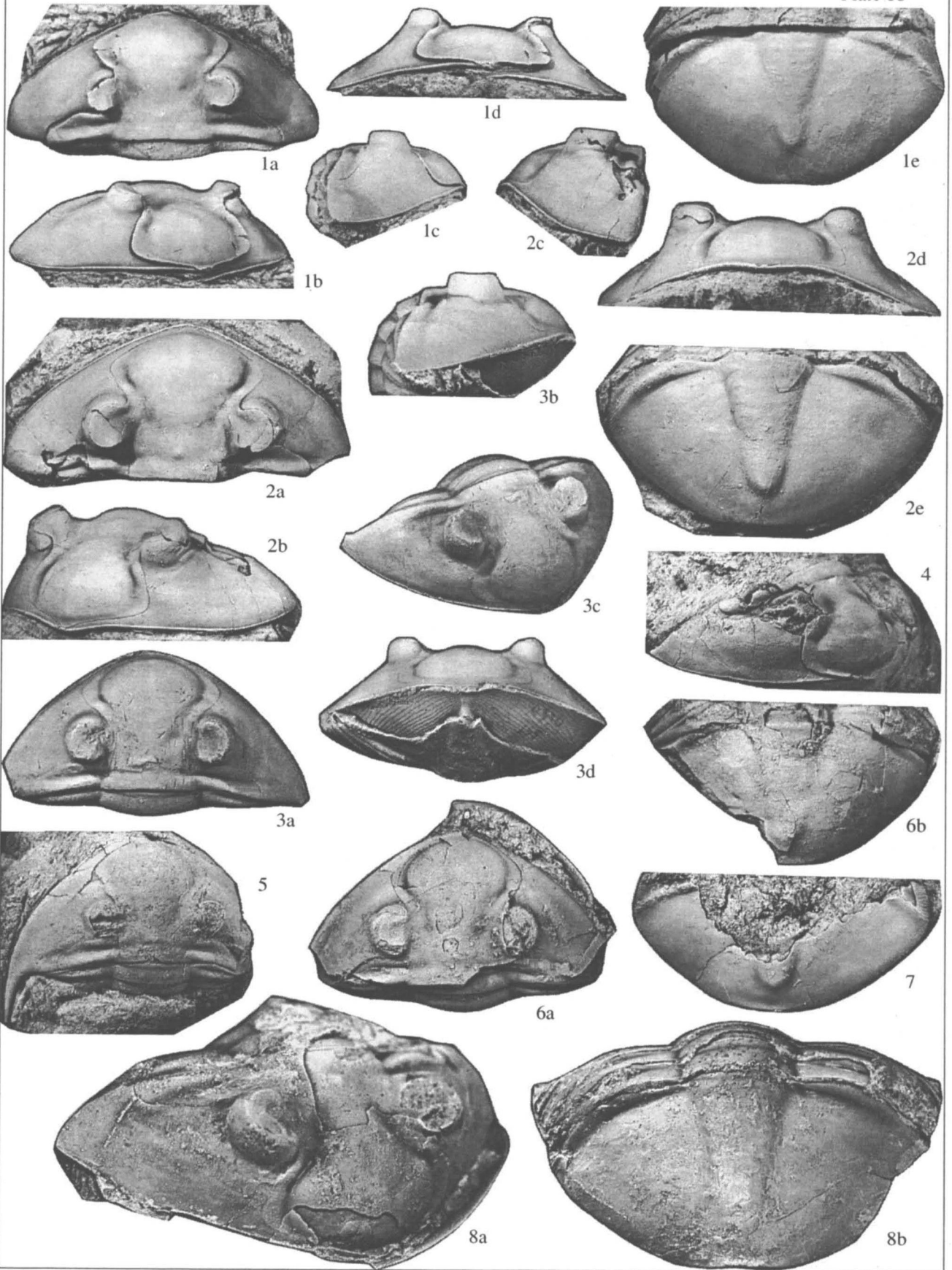
*Asaphus* (*Trematophorus*) *platyurus*: Balashova, 1953, pl. 3, fig. 1.

*Platysaphus spinifer*: Ivantsov, 2000, p. 52, pl. 9, figs. 2 and 3, text-figs. 2e and 2f.

**Holotype.** DPStPSU, no. 572/9243, unrolled carapace, designated and depicted by me (Ivantsov, 2000, pl. 9, figs. 2, 3), also depicted by Lesnikova (Lesnikova and Weber, 1949, pl. 69, fig. 4) and Balashova (1953, pl. 3, fig. 1); Volkhov River, outcrop near the Volkhov power station dam (Fig. 13); lower part of the Duboviki Formation, Middle Ordovician, Llanvirn, Aseri Horizon, *kotlukovi-punctatus* Zone (pl. 19, fig. 8).

**Diagnosis.** The eyes are of medium length, removed from the posterior margin at a distance equal to or a little greater than their length; palpebral lobes situated above the glabella; flexure between eye socle and librigena weak; genal spines present; occipital furrow absent; panderian organs neosaphine.

**Description.** The carapace is of medium size or large, the maximum measured width of the cephalon (at the level of the posterior margin of the occipital ring) is 56 mm. The cephalon is wide or of medium proportions (ratio of its length to its width is 0.44 in the holotype and 0.51 in the specimen no. 4330/170), weakly acuminate anteriorly, with a weak beaklike bend. The frontal lobe of the glabella is flattened, fall-



ing short of reaching the anterior margin, bordered anteriorly by a weak furrow. The medial lobe is weakly bordered laterally, the flexure between it and the frontal lobe is weak. The basal lobes are lenslike and weakly defined. The eyes are of medium length, low, removed from the posterior margin of the shield at a distance equal to or a little greater than their length, and closely spaced. The palpebral lobes are situated higher than the middle part of the glabella. The eye socles are underdeveloped, the flexure between the eye socle and the librigena is weak. The eye pedicles, eye lists, and tubercle in the posterolateral corners of the ocular areas are absent. The ocular areas are not elevated above the cephalon. The cranidium has a broad lingula. The dorsal furrows are distinct on the frontal lobe and weak or absent from the basal lobes. The glabellar furrows are shallow. The pseudodorsal furrows are weakly defined. The fossulae are clear. The paradoublural furrows are absent. The occipital furrow is absent. The occipital node is poorly defined. The librigenae are concave in their posterior parts, anteriorly with the outlined limb-like flexure. The genal corners possess long spines. The vincular pits are not expressed on the outer face. The occipital ring and rings of the body rachis are flat. The pygidium is wide (ratio of its length to its width is 0.5 in the holotype), with straightened lateral margins and a slightly obtuse posterior end. The rachis is weakly expressed, unsegmented, and weakly bordered posteriorly. The pleurae are flat and smooth and are not bordered behind the rachis. The D-folds are present on the anterior part of the frontal lobe of the glabella, on the librigenae near the genal corners, and on the spines. The panderian organs are neosaphine.

**C o m p a r i s o n.** This species is similar to *S. platyurus* (Angelin, 1858) and *S. latisegmentatus* (Nieszkowskii, 1857) in the presence of the genal corners; it differs from the first in the palpebral lobes being elevated above the glabella and the very weak flexure between the eye socle and the librigena. From *S. latisegmentatus*, it differs in its eyes being more distant from the posterior margin, in the absence of the occipital furrow, and in the weakly expressed flexure between

the librigena and the eye socle. It is similar to *S. laticaudatus* (F. Schmidt, 1901) in the weakly expressed flexure between the librigena and the eye socle, but it differs in the eyes being shorter and more distant from the posterior margin, in the absence of the occipital furrow, in the presence of the genal spines in adults, and in the neosaphine panderian organs.

**R e m a r k s.** Balashova (1953) proposed the holotype as the neotype of *Asaphus platyurus* Angelin, 1858. Since the type collection of Angelin has not survived (Jaanusson, 1953b), this is not correct.

**O c c u r r e n c e.** Middle Ordovician, Llanvirn, Aseri Horizon, *kotlukovi-punctatus* Zone and, possibly, beds with *A. intermedius*–*A. kowalewskii*; Duboviki Formation.

**M a t e r i a l.** Holotype and two carapaces PIN, nos. 4330/170 and 4330/171; Volkhov River, Duboviki Formation; Ruditsa River (1.6–1.9 m above the upper oolitic bed); village of Kotly.

*Subasaphus latisegmentatus* (Nieszkowskii, 1857)

Plate 18, figs. 3–8

*Asaphus latisegmentatus*: Nieszkowskii, 1857, p. 39 (part), pl. 2, fig. 1.

*Asaphus platyurus* var. *laticauda*: Schmidt, 1898, p. 21 (nom. nud.); 1901, p. 56, pl. 3, figs. 5 and 6.

*Asaphus laevisimus*: Schmidt, 1901, pl. 5, figs. 7, 7a, 8, and 13.

*Asaphus platyurus*: Schmidt, 1901, pp. 55–57, pl. 3, figs. 5 and 6, pl. 12, fig. 19, text-fig. 8; Lesnikova and Weber, 1949, pl. 69, fig. 5.

*Asaphus* (*Neoasaphus*) *platyurus latigena*: Jaanusson, 1953a, p. 393; Balashova, 1976, p. 13.

*Asaphus* (*Trematophorus*) *platyurus*: Balashova, 1953, p. 404, pl. 1, fig. 29 (?), pl. 3, fig. 1.

*Asaphus* (*Neoasaphus*) *platyurus latisegmentatus*: Jaanusson, 1953b, p. 475, pl. 2, figs. 4–6, pl. 3, figs. 1–4, text-fig. 4; Balashova, 1976, p. 13.

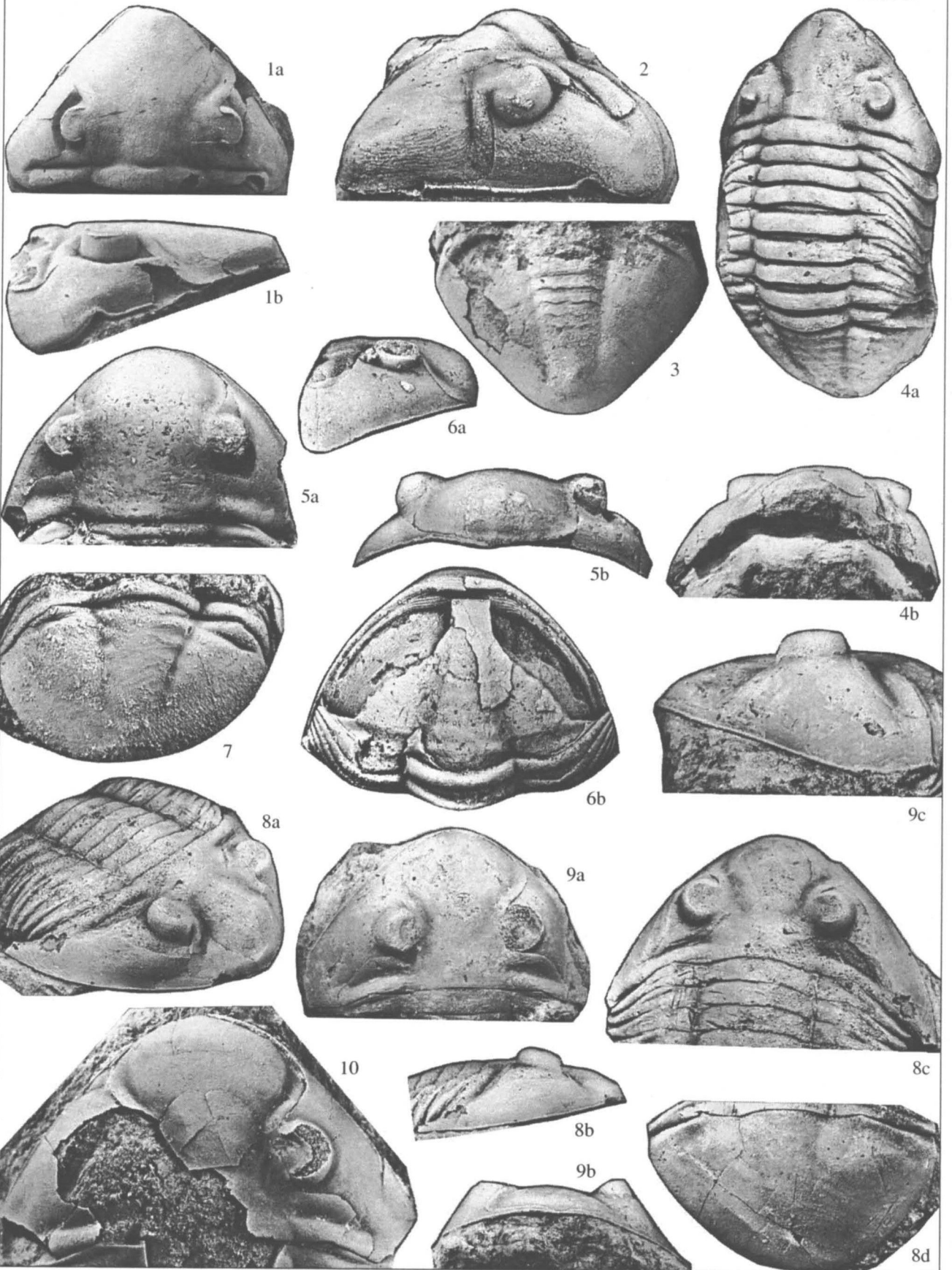
*Platysaphus latisegmentatus*: Ivantsov, 2000, figs. 2a–2c.

**L e c t o t y p e.** Unrolled carapace depicted by Nieszkowskii (1857, pl. 2, fig. 1), designated by Jaanusson (1953b); environs of the village of Kunda; Aseri Horizon.

Explanation of Plate 18

**Figs. 1 and 2.** *Subasaphus laticaudatus* (Schmidt, 1901): (1) specimen PIN, no. 4330/44, rolled carapace,  $\times 1$ : (1a–1c) cephalon (1a) dorsal view, (1b) half-turned view, (1c) side view, (1d) frontal view, (1e) pygidium; left bank of the Volkhov River, new auto-bridge in the town of Volkhov; Aseri Horizon, Simankovo Formation, Member 3, *heckeri* Zone, 1.9 m above ds4; (2) specimen PIN, no. 4330/89, rolled carapace,  $\times 1.5$ : (2a–2c) cephalon (2a) dorsal view, (2b) half-turned view, (2c) side view, (2d) frontal view, (2e) pygidium; Volkhov River, Volkhov power station dam outcrop; same stratigraphical position and age, talus.

**Figs. 3–8.** *Subasaphus latisegmentatus* (Nieszkowskii, 1857): (3) specimen PIN, no. 4330/155, rolled, partially destroyed carapace: (3a) dorsal view,  $\times 1.5$ ; (3b) side view,  $\times 2$ ; (3c) half-turned view,  $\times 1.5$ ; and (3d) frontal view,  $\times 1.5$ ; Volkhov River, stratigraphical position unknown; Lesnikova's collection; (4) specimen PIN, no. 4330/142, fragment of a small individual with underdeveloped genal spines,  $\times 1.5$ ; Lava River, Kavra outcrop; Aseri Horizon, Simankovo Formation, Member 3, *heckeri* Zone, 0.2 m above ds4; (5) specimen PIN, no. 4330/92, cephalon with left gena partially missing,  $\times 1.5$ ; left bank of the Volkhov River, near the railroad bridge in the town of Volkhov; same stratigraphical position and age, talus; (6) specimen PIN, no. 4330/90, rolled carapace fragment,  $\times 1.5$ : (6a) cephalon, (6b) pygidium; Volkhov River, Volkhov town, near the railroad bridge; same stratigraphical position and age, 5 m above the roof of the Sinyavino Formation; collected by Balashova; (7) specimen PIN, no. 4330/91, fragment of shortened pygidium,  $\times 2$ ; Volkhov River; same age; collected by Balashova; (8) specimen PIN, no. 4330/182, rolled carapace of an individual possessing genae without spines and a short pygidium, like *Subasaphus laticaudatus*: (8a) cephalon half-turned view,  $\times 2.5$ ; (8b) pygidium,  $\times 2$ ; Volkhov River, Volkhov power station dam outcrop, same stratigraphical position and age, 0.95 m above ds4.



**Diagnosis.** Eyes are of medium length, located slightly nearer than their length to the posterior end; palpebral lobes are elevated above the glabella; flexure between eye socle and librigena is usually present; genal spines present; occipital furrow shallow, developed along its entire length; panderian organs neosaphine.

**Description.** The carapace is of medium size or large, the maximum measured width of the cephalon is 55 mm. The cephalon is wide (mean  $l/d$ , 0.43), weakly acuminate anteriorly, with weak beaklike bend. The frontal lobe of the glabella is moderately convex, with the maximum in the anterior part, not reaching the anterior margin, bordered anteriorly by a sharp furrow, and bearing a weak longitudinal ridge. The medial lobe is weakly bordered laterally, the flexure between it and the frontal lobe is weak. The basal lobes are lenslike and weakly defined. Rudiments of the glabellar lobes are present. The eyes are of medium length, low, shifted slightly less than their length to the posterior margin of the shield, and closely spaced (mean  $lo/l$ , 0.33; mean  $ho/lo$ , 0.47; mean  $la/lp$ , 1.6; and mean  $do/d$ , 0.51). The eye socles are underdeveloped. The palpebral lobes are elevated above the middle part of the glabella. The flexure between the eye socle and the librigena is usually present. The eye pedicles, eye lists, and tubercle in the posterolateral corners of the ocular areas are absent. The ocular areas are not elevated above the cephalon. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is rounded, and the anterior bend is distinct. The cranidium has a broad lingula. The distance between the facial sutures at the level of the marginal bends is greater than that at the level of the eye socles. The maximum width of the anterior part of the fixed gena is situated near the anterior margin of the shield. The dorsal furrows are distinct on the frontal lobe and weak or absent from the basal lobes. The glabellar furrows are shallow. The pseudodorsal furrows are weakly defined. The occipital furrow is shallow and well-developed along its entire length. The fossulae are clear. The paradoublural fur-

rows are absent. The occipital node is poorly defined. The librigenae are weakly concave in their posterior parts and show a poorly defined limblike flexure anteriorly. The genal corners bear long spines. The vincular pits are not expressed on the outer face. The occipital ring is flat. The rings of the body rachis are flat to weakly convex. The pygidium is wide (mean  $L/D$ , 0.52), with straightened lateral margins and a slightly obtuse posterior end. The pattern of segmentation of the outer surface of the pygidial rachis is not defined, its cast is segmented along its entire length. The rachis is abruptly bordered posteriorly. The pleurae are flat, smooth, and not bordered behind the rachis. The D-folds are present on the anterior part of the frontal lobe of the glabella (weak), on the librigenae near the genal corners and on the spines, and on the anterolateral margins of the pygidial pleurae. The panderian organs are neosaphine.

**Variability.** The genal spines, one of the distinctive characters of the species, may be underdeveloped (Pl. 19, fig. 4) or entirely absent (Pl. 19, fig. 8). There are specimens possessing a gentle, almost unbent, transition between the optical surface and the librigena. The width of the pygidium and the degree of the straightening of its posterior margin also vary.

**Comparison.** This species is similar to *S. platyrus* (Angelin) in the presence of genal spines and a characteristically developed flexure between the eye socle and the librigena and differs in the eyes being closer to the posterior margin of the cephalon, palpebral lobes elevated above the glabella, and in the presence of the occipital furrow. It is similar to *S. laticaudatus* in the eyes being removed from the posterior margin of the shield at the same distance, in the tendency toward a shallower flexure between the librigena and the eye socle in some specimens of *S. latisegmentatus*, and in the presence of an occipital furrow and underdeveloped genal spines in some specimens but differs in the shorter eyes, genal spines common in adults, and the flexure between the librigena and the eye socle; the most striking difference is the structure of the panderian

#### Explanation of Plate 19

**Figs. 1–4.** *Delphasaphus delphinus* (Lawrow, 1856): (1) specimen PIN, no. 4330/130, cephalon: (1a) dorsal view,  $\times 1$ ; (1b) side view,  $\times 1.5$ ; Volkhov River, Volkhov power station dam outcrop; Aseri Horizon, Duboviki Formation, the beds with *A. intermedius*–*A. kowalewskii*, 7.65 m above ds4; (2) specimen PIN, no. 4330/131, cephalon,  $\times 1.5$ ; same age and locality; (3) specimen PIN, no. 4330/132, incomplete pygidium,  $\times 1.2$ ; Volkhov River, Volkhov town, stratigraphical position unknown; collected by Lesnikova, 1928; (4) lectotype StPSMI, no. 56/6, unrolled, partially destroyed carapace: (4a) general appearance,  $\times 1$ ; (4b) frontal view,  $\times 1.5$ ; village of Ropsha; stratigraphical position unknown; N. Lawrow's collection.

**Figs. 5–7.** *Onchometopus volborthi* F. Schmidt, 1898: (5) specimen PIN, no. 4330/148, incomplete cephalon,  $\times 1.5$ : (5a) dorsal view, (5b) frontal view; Putilovo outcrop; Volkhov Horizon, Zheltyaki Member, beds with *A. ? broeggeri*, dump; (6) specimen PIN, no. 4330/146, rolled, partially destroyed carapace,  $\times 1.5$ : (6a) cephalon, side view, (6b) caudal view demonstrating the purpose of the groove on the cephalon doublure, which serves as a stop for folded pleura of the body and for the pygidium margin when a trilobite is rolled up; same age and locality; (7) specimen PIN, no. 4330/147, pygidium,  $\times 2$ ; same age and locality.

**Figs. 8–10.** *Subasaphus spinifer* (Ivantsov, 2000): (8) holotype DPStPSU, no. 572/9243, unrolled, slightly deformed carapace with genal spines missing,  $\times 1$ : (1a–1c) cephalon (8a) half-turned view, (8b) side view, (8c) dorsal view; (8d) pygidium; Volkhov River, Volkhov power station dam outcrop; Aseri Horizon, lower part of the Duboviki Formation, *kotlukovi*–*punctatus* Zone; collected by Hecker; (9) specimen PIN, no. 4330/170, incomplete cephalon: (9a) dorsal view,  $\times 1$ ; (9b) frontal view,  $\times 1$ ; (9c) side view,  $\times 1.5$ ; Volkhov River, Volkhov town; Volkhovstroi Subhorizon; collected by Balashova; (10) specimen PIN, no. 4330/178, incomplete cephalon,  $\times 1.5$ ; left bank of the Volkhov River near the railroad bridge; Aseri Horizon, talus.

rian organs, which are neoasaphine in the species under consideration.

**Remarks.** Schmidt designated in 1898 and described and depicted in 1901 *A. platyurus* var. *laticauda* (Schmidt, 1898, 1901). Jaanusson (1953a) considered it a homonym of *A. laevissimus* var. *laticauda*, proposed a new name *A. (Neoasaphus) platyurus latigena*, and, subsequently, treated it as a junior synonym of *A. latisegmentatus* (Jaanusson, 1953b). Balashova (1976) reinstated the first name and indicated characters differentiating Schmidt's subspecies from Nieszkowskii's species. The depository of the originals by Nieszkowskii is unknown. Among three figures published by him (Nieszkowskii, 1857, pl. 2, figs. 1–3), one is a drawing of the carapace fragment (gena, part of the body shield, and pygidium) lying on a rock (fig. 1), the second is a reconstruction of a body segment (fig. 2), and the third is a reconstruction of the cephalon (fig. 3). A representative of the family Ptychopygidae (widely bordered, swollen frontal lobe, and narrow and closely set eyes) is most probably depicted on the third drawing. The specimen on the first figure was treated by Jaanusson as the lectotype of the species. Despite the fragmentary preservation of the specimen and the poor quality of the figure, it may be allocated with high probability to the same species as *A. platyurus* var. *laticauda*. Judging from the characters mentioned by Balashova, she pointed out differences between the forms based on a reconstruction of a cephalon different from those of *Asaphus* and *Subasaphus*.

This species is morphologically similar to *A. heckeri*, with which it occurs in association, in the shortened and anteriorly acuminate cephalon, low eyes, same development of the furrows, flat occipital ring, posteriorly concave librigenae, shortened pygidium, weak development of the terracelike folds, and in the neoasaphine panderian organs but differs in the absence of the eye lists and tubercles from the posterolateral corners of the ocular areas and in the presence of genal spines.

**Occurrence.** Middle Ordovician, Llanvirn, Aseri Horizon, lower part of the *heckeri* Zone; Simankovo Formation, Member 3. Outside the Ladoga Glint: Baltic Glint, Leningrad Region, lower part of the Duboviki Formation; Estonia, Aseri (?) Formation.

**Material.** Twenty-five specimens: Volkhov River, 0–0.9 m above ds4; Lava River, 0.2 m above ds4; village of Putilovo.

*Subasaphus laticaudatus* (Schmidt, 1901)

Plate 18, figs. 1 and 2; Plate 21, fig. 10

*Asaphus laevissimus* var. *laticauda*: Schmidt, 1901, p. 61, pl. 5, figs. 10a and 10b, text-fig. 6.

*Asaphus laevissimus*: Schmidt, 1901, pl. 5, fig. 11 (?).

*Asaphus (Neoasaphus) laevissimus* var. *laticauda*: Jaanusson, 1953a, p. 398.

*Asaphus (Trematophorus) laticaudatus*: Balashova, 1953, p. 412, pl. 3, figs. 2 and 3.

*Asaphus (Subasaphus) laticaudatus*: Balashova, 1976, p. 11.

**Lectotype.** GMAGI, no. 55/11152, unrolled carapace, depicted by Schmidt (1901, pl. 5, figs. 10a, 10b), designated by Balashova (1953); village of Gostilitsy; substage C<sub>1a</sub>.

**Diagnosis.** Eyes long, less than their length away from posterior margin; palpebral lobes elevated above glabella; flexure between eye socle and librigena and genal spines absent; occipital furrow shallow and well-developed along its entire length; panderian organs subasaphine.

**Description.** The carapace is of medium size or large, the maximum measured width of the cephalon is 58.5 mm; mean d, 40.5 mm. The cephalon is wide (mean l/d, 0.43), weakly acuminate anteriorly, with or without a weak beaklike bend. The frontal lobe of the glabella is strongly convex, with the maximum convexity in the middle part, reaching the anterior margin, bordered by a sharp furrow anteriorly, and bearing a weak longitudinal ridge. The medial lobe is weakly bordered laterally, the flexure between it and the frontal lobe is weak or absent. The basal lobes are lenslike and weakly defined. Rudiments of the glabellar lobes are present. The eyes are long and low and situated less than their length away from the posterior margin of the shield and are moderately separated (mean lo/l, 0.35; mean ho/lo, 0.56; mean la/lp, 1.4; and mean do/d, 0.55). The eye socles are underdeveloped. The palpebral lobes are higher than the middle part of the glabella. The flexure between the eye socle and the librigena is absent. The eye pedicles, eye lists, and tubercle are absent from the posterolateral corners of the ocular areas. The ocular areas are not elevated above the cephalon. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent, the marginal bend is sharp and angular, and the anterior bend is distinct. The cranium has a broad lingula. The distance between the facial sutures at the level of the marginal bends is greater than that at the level of the eye socles. The maximum width of the anterior part of the fixed gena is situated near the anterior margin of the shield. The dorsal furrows are distinct on the frontal lobe and weak or absent from the basal lobes. The glabellar furrows are shallow. The pseudodorsal furrows are weakly defined. The occipital furrow is shallow and well-developed along its entire length. The fossulae are unclear. The paradoublural furrows are absent. The occipital node is distinct. The librigenae are concave in their posterior parts. The genal corners are obtuse and lack spines. The vincular pits are not expressed on the outer face. The occipital ring is flat and the rings of the body rachis are flat. The pygidium is very wide (mean L/D, 0.5) and has straightened lateral margins and an obtuse posterior end. The pygidial rachis is weakly segmented (three or four segments are visible) and weakly bordered posteriorly. The pleurae are flat, smooth, and not bordered behind the rachis. The D-folds are present on the anterior part of the frontal lobe of the glabella (weak), on the librigenae near the genal corners, and on the antero-

lateral margins of the pygidial pleurae. The panderian organs are subasaphine.

**Comparison.** It differs from all species of the genus *Subasaphus* in the gentle transition between the eye surface and the librigena and in the subasaphine panderian organs. The comparison with other characters of *S. latisegmentatus* is given under the description of the latter species.

**Remarks.** Schmidt's original has survived; therefore, the designation of the specimen DPStPSU, no. 575/9243 as the neotype is incorrect (Balashova, 1953). This species is morphologically similar to species of the genus *Asaphus*, *A. laevissimus* and *A. heckeri*. It resembles *A. heckeri* in the shortened, anteriorly acuminate cephalon, posteriorly concave librigenae, low eyes, weak development of the glabellar and occipital furrows, flat occipital ring, and weak terracelike folds, but differs in the larger eyes and the absence of the eye lists and tubercles from the posterolateral corners of the ocular areas. The comparison with *A. laevissimus* is given under the description of the latter species.

**Occurrence.** Middle Ordovician, Llanvirn, Aseri Horizon, upper part of the *heckeri* Zone; Simankovo Formation, Member 3. Outside the Ladoga Glint: Baltic Glint, Leningrad Region, lower part of the Duboviki Formation; Estonia, Aseri (?) Formation.

**Material.** Fifty-two specimens: Volkhov River, 0.7–1.45 m above ds4; Lava River, 1.65 m above ds4; village of Putilovo.

### Genus *Xenasaphus* Jaanusson, 1953

*Xenasaphus*: Jaanusson, 1953a, p. 459; 1959, p. 339; Balashova, 1960, p. 143; 1976, p. 23.

*Xenasaphus* (*Xenasaphus*): Ivantsov, 2000, p. 54.

**Type species.** *Asaphus devexus* Eichwald, 1840.

**Diagnosis.** Cephalon elongated, basal lobes present; eyes low; eye pedicles absent; palpebral lobes usually lower than middle part of glabella; genal corners rounded; narrow bordering present in front of glabella; vincular apparatus represented on cephalon by deep pits; pygidium elongated, rachis coarsely segmented, segments not interrupted at its axis, with wide concave bordering; panderian organs neoasaphine (?).

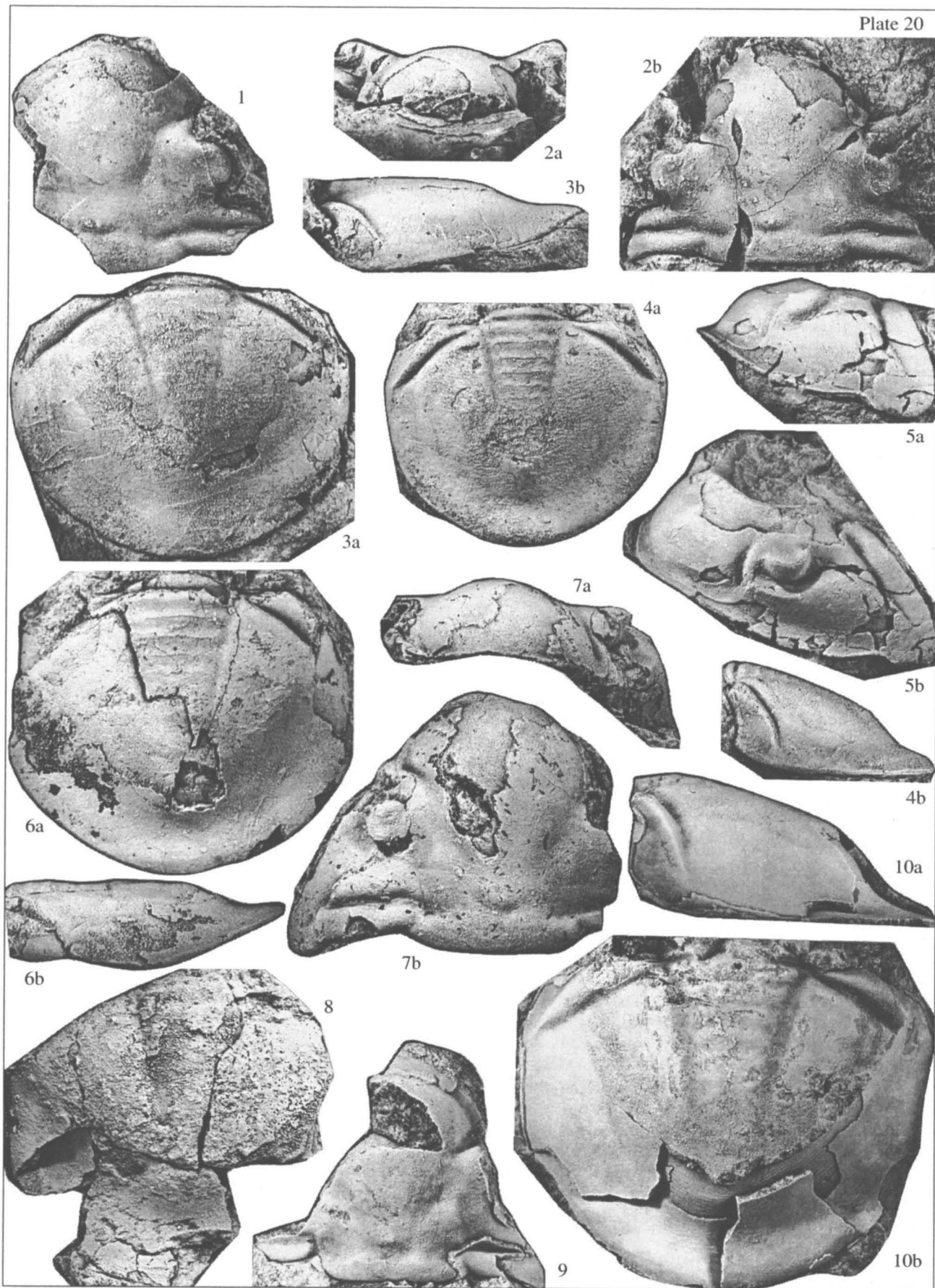
**Description.** The carapace is large and, occasionally, very large, the maximum measured widths of the cephalon and pygidium are 88 and 86 mm, respectively. The cephalon is elongated and anteriorly acuminate, without a beaklike bend, with straightened lateral margins. The glabella is divided into a very large pear-shaped frontal lobe, a small rectangular medial lobe, and basal lobes. The frontal lobe of the glabella is moderately or strongly convex, with the maximum convexity in the anterior or middle part, far from reaching the anterior margin, anteriorly bordered by a sharp furrow, and lacking the longitudinal ridge. The medial lobe is clearly bordered laterally, the flexure between it and the frontal lobe is weak and is usually absent. The basal

lobes are lenslike and moderately expressed. Rudiments of the glabellar lobes and the occipital node are absent. The dorsal furrows are sharp in the frontal and basal lobes. The glabellar furrows are shallow and usually fused with small pseudodorsal furrows. The fossulae are distinct. The occipital furrow is shallow and well-developed along its entire length or shaped like a pit. The paradoublural furrows are absent. The occipital ring is flat. The anterior branches of the facial sutures run parallel to the anterior margin along most of their length and approach it; the ocular bend of the anterior branch is absent, the marginal bend is rounded. The distance between the facial sutures at the level of the marginal bends is a little greater than that at the level of the eye socles. The cranidium is acuminate anteriorly and lacks the lingula. The anterior part of the fixed gena is widest near the eye. The eyes are small, of medium height, approaching to the anterior or posterior margin of the shield, and widely separated. The palpebral lobes are either lower or higher than the posterior part of the frontal lobe. The eye socles are underdeveloped. The eye lists are weakly expressed. The eye pedicles are absent. The ocular areas are not elevated above the cephalon, their posterior margins are devoid of ridges and tubercles. The librigenae are convex and bear a narrow bordering that starts from the anterior margins of the vincular pits. The genal corners are rounded. The vincular pits are deep and expressed on the outer surface as deep gentle incisions of the lateral margin. The occipital ring and the rings of the body rachis are flat. The pygidium is of medium length and elongated, with rounded lateral margins and a rounded posterior end. The rachis is wide, segmented (segments are not interrupted at its axis) and weakly bordered posteriorly. The pleurae are convex, smooth, with a wide concave bordering. The vincular tubercles are absent. The facets widen toward the lateral corners of the pygidium. The D-folds are rather coarse; they emphasize segmentation on the anterior part of the frontal lobe of the glabella, anterior parts of the fixed genae, rings of the body rachis, and pygidial rachis and are transverse on the pleurae. The panderian organs are neoasaphine (?).

**Species included.** *X. devexus* (Eichwald, 1840) and *X. mjannili* Ivantsov, 2000.

**Comparison.** From the genera *Asaphus*, *Subasaphus*, and *Onchometopus*, it differs in the bordered cephalon and pygidium. The comparison with the genus *Delphasaphus* is given under the description of the latter.

**Remarks.** The genus *Xenasaphus* is postulated to be distributed in the Uhaku Horizon only (Balashova, 1953, 1976; *Resheniya...*, 1987). On the Volkhov River, I found a pygidium of *Xenasaphus* sp. (Pl. 20, fig. 8) in association with remains of *A. bottnicus* and *A. (?) ornatus* in deposits of the Lasnamägi age. Pygidia found by L.E. Popov on the Koporka River (personal communication) appear to come from deposits of the same age.



**Occurrence.** Baltic–Ladoga Glint; Middle Ordovician, Llanvirn, Llandeilo, Lasnamägi and Uhaku horizons, beds with *A. bottnicus* and with *Xenasaphus*.

*Xenasaphus devexus* (Eichwald, 1840)

Plate 20, figs. 5–7, 9, 10

*Asaphus devexus*: Eichwald, 1840, p. 79; Eichwald, 1861, p. 43, pl. 32, fig. 10; Schmidt, 1898, p. 25; 1901, p. 65, pl. 7, figs. 1–6, text-fig. 9; Lesnikova and Weber, 1949, p. 284, pl. 64, figs. 1–5.

*Asaphus devexus* var. *applanata*: Schmidt, 1901, pl. 7, fig. 7.

*Xenasaphus devexus*: Jaanusson, 1953a, p. 459; Balashova, 1976, p. 23.

*Asaphus (Trematophorus) devexus*: Balashova, 1953, p. 417, pl. 3, figs. 6 and 7.

*Asaphus (Trematophorus) devexus* var. *applanata*: Balashova, 1953, pl. 5, fig. 1.

*Xenasaphus applanatus*: Balashova, 1976, p. 23.

*Xenasaphus (Xenasaphus) devexus*: Ivantsov, 2000, p. 54, pl. 9, figs. 5–7, text-figs. 3a and 3b.

**Lectotype.** DHGStPSU, no. 1/1212, pygidium, depicted by Eichwald (1861, pl. 32, fig. 10) and designated by me (Ivantsov, 2000); Odenscholm; age not indicated (Pl. 20, fig. 10).

**Diagnosis.** Eyes closer to anterior margin of cephalon than to posterior margin; palpebral lobes lower than glabella; flexure between frontal and medial lobes absent; occipital furrow shaped like isolated pit.

**Description.** The trilobites are large and very large, the maximum measured width of the cephalon (specimen PIN, no. 4330/133) is 88.0 mm. The cephalon is elongated (*l/d*, 0.57), anteriorly acuminate, with a weak beaklike bend on the anterior margin. The frontal lobe is moderately convex, with the maximum convexity in the anterior and middle parts, far from reaching the anterior margin, and bordered anteriorly by a sharp furrow. The flexure between the frontal and medial lobes is absent. The medial lobe is weakly bordered laterally. The basal lobes are lenslike and moderately expressed. Rudiments of the glabellar lobes, a keel-like ridge, and the occipital node are absent. The dorsal furrows are sharp in the frontal and basal lobes, the glabellar lobes are shallow. The fossulae are distinct. The occipital furrow is pitlike. The occipital ring is flat. The bends of the anterior branch of the facial

suture are as follows: the ocular bend is absent and the marginal bend is rounded. The distance between the facial sutures at the level of the marginal bends is slightly greater than that at the level of the eye socles. The anterior part of the fixed gena is widest near the eye. The cranium is acuminate anteriorly. The librigenae are convex. The eyes are small, of medium height, closer to the anterior end, and widely separated (mean *lo/l*, 0.19, mean *ho/lo*, 0.7; mean *la/lp*, 0.72; and mean *do/d*, 0.64). The palpebral lobes are situated lower than the middle part of the glabella. The eye socles are underdeveloped; the eye pedicles and tubercles in the posterolateral corners of the ocular areas are absent; the eye lists are weakly expressed. A narrow bordering limited posteriorly by incisions of the vincular pits is present. The paradoublural furrows are absent. The vincular pits are deep and are shaped on the outer surface of the gena as a deep and gently sloping excavation. The genal corners are rounded. The rings of the body rachis are weakly convex. The pygidium is elongated (*L/D*, specimen PIN, no. 4330/135, 0.76), with rounded lateral margins. The rachis is coarsely segmented, the segments are not interrupted at its axis (four or five visible segments) and are poorly defined posteriorly. The pleurae are convex and smooth. A wide, concave bordering is present. The vincular tubercles are absent. The D-folds being hardly noticeable on the typically leached carapace are present on the anterior part of the frontal lobe of the glabella and on the rings of the body rachis (coarse), on the pygidial rachis (emphasizing segmentation), and on the pygidial pleurae (transverse). The panderian organs are neoasaphine (?).

**Variability.** The carapace convexity varies.

**Comparison with *X. mjannili*** is given under the description of the latter species.

**Remarks.** Balashova (1976) established a separate species, *X. applanatus*, for the form with a somewhat flatter pygidium. In this case, the flattened pygidium seems inadequate to establish a species, since carapaces possessing more convex, as well as flatter, pygidia may be recorded in the same locality, bed, and aggregation. It cannot be excluded that we are dealing with a rare case of sexual dimorphism.

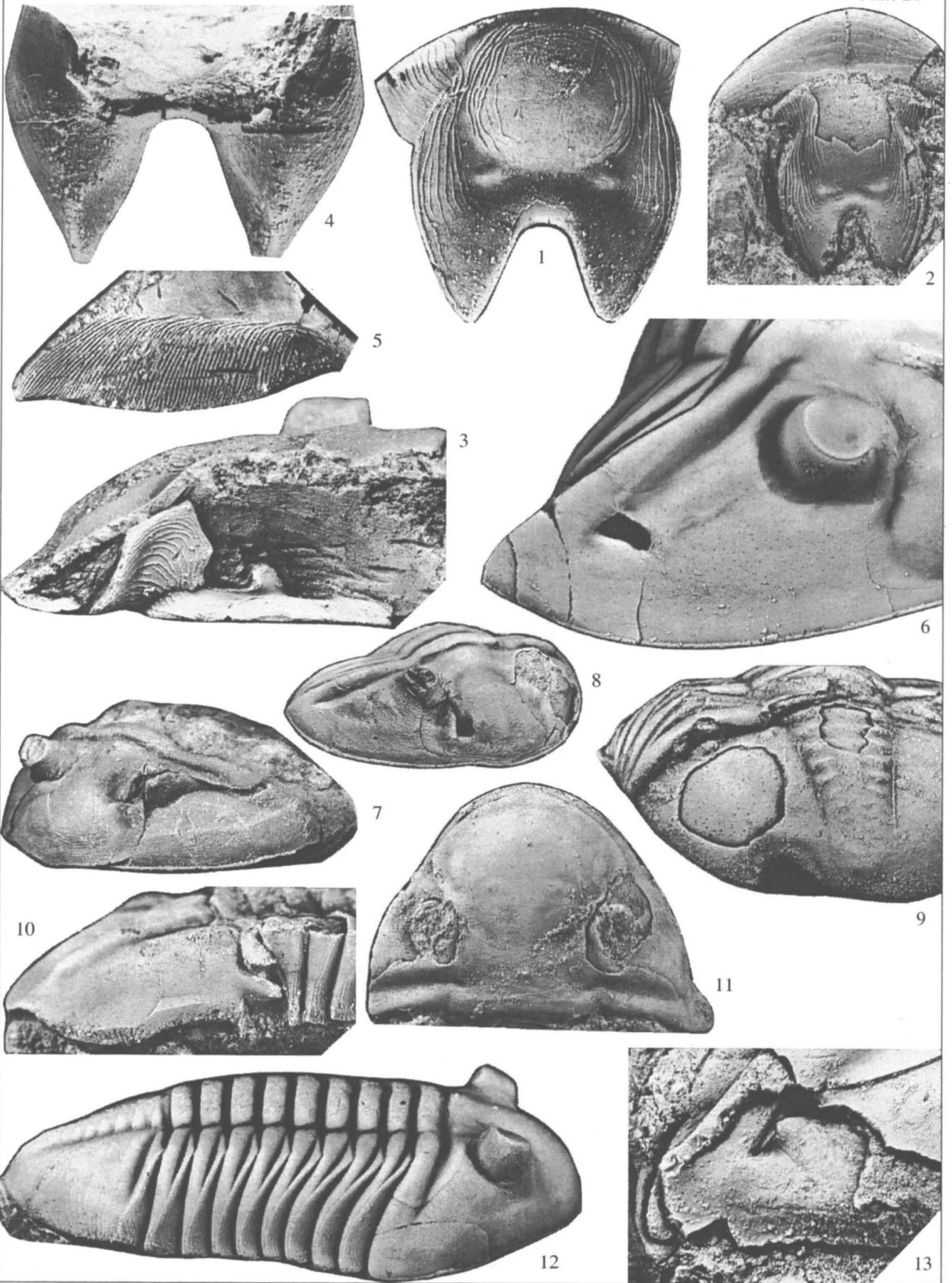
Explanation of Plate 20

**Figs. 1–4.** *Xenasaphus mjannili* Ivantsov, 2000: (1) specimen PIN, no. 4330/137, incomplete cranidium,  $\times 1$ ; (2) holotype PIN, no. 4330/136, cranidium,  $\times 1$ : (2a) frontal view, (2b) dorsal view; (3) specimen PIN, no. 4330/139, flattened pygidium,  $\times 0.75$ ; (4) specimen PIN, no. 4330/138, relatively more convex pygidium,  $\times 0.75$ : (4a) dorsal view, (4b) side view; Volkhov River, Porogi–Valim outcrop; Uhaku Horizon, Valim Formation, lower part of the beds with *Xenasaphus*, 10.2–10.3 m above the floor of the Porogi Formation.

**Figs. 5–7.** *Xenasaphus devexus* (Eichwald, 1840): (5) specimen PIN, no. 4330/133, incomplete cephalon,  $\times 0.75$ : (5a) lateral view, (5b) half-turned view; Volkhov River, Porogi–Valim outcrop; Uhaku Horizon, Valim Formation, beds with *Xenasaphus*, 14.1–14.2 m above the floor of the Porogi Formation; (6) specimen PIN, no. 4330/135, pygidium with partially destroyed carapace,  $\times 0.75$ : (6a) dorsal view, (6b) side view; same age and locality; (7) specimen PIN, no. 4330/134, incomplete cephalon,  $\times 1$ : (7a) frontal view, (7b) dorsal view; same age and locality.

**Fig. 8.** *Xenasaphus* sp. specimen PIN, no. 4330/129, pygidium fragment with leached carapace,  $\times 1$ ; Volkhov River, Shkurina Gorka outcrop, the beds with *A. bottnicus*, 5.1 m above the floor of the Porogi Formation.

**Figs. 9 and 10.** *Xenasaphus devexus* (Eichwald, 1840) specimens from Eichwald's collection,  $\times 1$ ; Baltic Glint, Estonia, Odenscholm; stratigraphical position unknown: (9) specimen HGDStPSU, no. 1/1211, fragment of cranidium imprint; (10) lectotype HGDStPSU, no. 1/1212, pygidium fragment.



The lectotype selected by Balashova (1953) in Schmidt's collection is invalid, since it does not belong to Eichwald's originals.

**Occurrence.** Within the Ladoga Glint, this species has only been recorded on the Volkhov River in deposits of the Valim Formation, upper part of the beds with *Xenasaphus*. Outside the Ladoga Glint: Baltic Glint, Leningrad Region, Valim (?) Formation (Balashova, 1953, 1976); Estonia, Vao Formation (TMN).

**Material.** Forty-eight specimens: Volkhov River, Valim Formation, 14.1–14.2 m above the floor of the Porogi Formation.

*Xenasaphus mjannili* Ivantsov, 2000

Plate 20, figs. 1–4

*Xenasaphus (Xenasaphus) mjannili*: Ivantsov, 2000, p. 55, pl. 9, figs. 8–10, text-figs. 3c and 3d.

**Holotype.** PIN, no. 4330/136, cranidium, designated by me (Ivantsov, 2000, pl. 9, figs. 8–10); Volkhov River, Porogi–Valim outcrop (Fig. 16b); Uhaku Horizon, Valim Formation, 10.2–10.3 m above the floor of the Porogi Formation; lower part of the beds with *Xenasaphus* (Pl. 20, fig. 2).

**Diagnosis.** Eyes closer to posterior margin than to anterior margin of shield; palpebral lobes elevated above glabella; flexure between frontal and medial

lobes present; occipital furrow well-developed along its entire length.

**Description.** Trilobites are large. The cephalon is elongated (l/d, 0.57). The frontal lobe is convex, with the maximum convexity in the anterior part, far from reaching the anterior margin, bordered anteriorly by a sharp furrow. The flexure between the frontal and medial lobes is distinct, the medial lobe is weakly bordered laterally. The basal lobes are lenslike and moderately convex. Rudiments of the glabellar lobes and the keel-like ridge are absent. The occipital node is absent. The dorsal furrows are sharp in the frontal and basal lobes, the glabellar lobes are shallow. The fossulae are distinct. The occipital furrow is shallow and well-developed along its entire length. The occipital ring is flat. The bends of the anterior branch of the facial suture are as follows: the ocular bend is absent and the marginal bend is rounded. The distance between the facial sutures at the level of the marginal bends is slightly greater than that at the level of the eye socles. The anterior part of the fixed gena is widest near the eye. The cranidium is acuminate anteriorly. The eyes are widely separated, removed from the posterior marginal furrow at a distance equal to their length. The palpebral lobes are elevated above the glabella, the eye pedicles are absent, the eye lists are weakly expressed. The rings of the body rachis are weakly convex. The pygidium is of medium length (mean L/D, 0.78), with rounded lateral

Explanation of Plate 21

**Fig. 1.** The form of the hypostome of trilobite of the subfamily Asaphinae is unusual due to projections developed at the posterior margin of the bordering; *Asaphus lepidurus* Nieszkowskii, 1859, specimen PIN, no. 4330/3,  $\times 4.5$ ; Putilovo outcrop, Volkhov Formation, dump.

**Fig. 2.** Standard for trilobites attachment of the hypostome by its anterior margin to the doublure, *Asaphus raniceps* Dalman, 1828, specimen PIN, no. 4330/156,  $\times 2$ ; Lava River, Gorodishchenskii Kar'er outcrop; Kunda Horizon, Obukhovo Formation, Member 1, *raniceps*–*striatus* Zone, 0–0.15 m above the floor.

**Fig. 3.** Additional articulation of the anterior flange of the hypostome with the inner face of the carapace of the asaphid cephalon, which strengthen the attachment, *Asaphus acuminatus lamanskii* F. Schmidt, 1901, specimen PIN, no. 4330/1,  $\times 5$ .

**Fig. 4.** *Asaphus knyrkoi* F. Schmidt, 1901, specimen PIN, no. 4330/6, inner side of the wedgelike processes of the hypostomal bordering,  $\times 5$ .

**Fig. 5.** Terracelike folds on the inner facet of the wedgelike process of the hypostomal bordering, which is supposedly a part of the grinding apparatus (Ivantsov, 1990b), *Asaphus* sp., specimen PIN, no. 4330/5,  $\times 9$ , defect.

**Figs. 6–10.** Lifetime (repaired) defects of the asaphid carapace: (6) perforation of the posterior margin of the *Asaphus laevisimus* F. Schmidt, 1901 librigena, specimen PIN, no. 4330/122,  $\times 3$ ; Volkhov River, Volkhov power station dam outcrop; Kunda Horizon, Simankovo Formation, Member 2, *laevisimus* Zone, talus; (7) *Asaphus kowalewskii* Lawrow, 1856 cephalon with a broken left eye pedicle, specimen PIN, no. 4330/149,  $\times 2$ ; left bank of the Volkhov River, Volkhov town, near the railroad bridge; Aseri Horizon, Duboviki Formation, beds with *A. intermedius*–*A. kowalewskii*; collected by M. Anosov and V. Zakharov; (8) perforation of the frontal lobe of the *Asaphus kowalewskii* Lawrow, 1856 glabella, specimen PIN, no. 4330/150,  $\times 1.5$ ; same age and locality; collected by M. Legeev; (9) incision on the posterior margin of the *Asaphus expansus robustus* subsp. nov. pygidium, specimen PIN, no. 4330/151,  $\times 3$ ; eastern part of the Ladoga Glint; Kunda Horizon, lower part of the Lynna Formation, collected by Balashova; (10) two incisions on the right margin of the pygidium and two last right pleura of *Subasaphus laticaudatus* (Schmidt, 1901) being cut, specimen PIN, no. 4330/180,  $\times 3$ ; Lava River, Kavra outcrop; Aseri Horizon, Simankovo Formation, Member 3, *heckeri* Zone, 1.4 m above ds4.

**Fig. 11.** Rudimentary lobes of the glabella (low elongated tubercles in the posterior part of the frontal lobe near the eyes), *Asaphus raniceps* Dalman, 1828, specimen PIN, no. 4330/156,  $\times 2$ .

**Fig. 12.** Gradual straightening of the posterior margin of the body pleurae from the anterior pleura to the posterior pleura, *Asaphus lepidurus* Nieszkowskii, 1859, specimen PIN, no. 4330/174,  $\times 2$ ; Lava River, Gorodishchenskii Kar'er outcrop; Volkhov Horizon, Volkhov Formation, Frizy Member, beds with *A. lepidurus*, about 1 m below the formation roof.

**Fig. 13.** Insertion of the anterior margin of the pleura of the first body segment into the incision of the panderian organ of the cephalon, which prevents tighter rolling of the carapace (Balashova, 1955), *Subasaphus spinifer* (Ivantsov, 2000), specimen PIN, no. 4330/170,  $\times 4$ ; Volkhov River, Volkhov town; Volkhovstroi Subhorizon; collected by Balashova.

margins. The rachis is coarsely segmented, the segments are not interrupted at its axis (five or six segments are visible), and are poorly defined posteriorly. The pleurae are convex and smooth. A wide concave border is present. The vincular tubercles are absent. Coarse D-folds are present on the anterior part of the frontal lobe of the glabella, the fixed gena, and on the rings of the body rachis; these folds emphasize segmentation on the pygidial rachis and are transverse on the pygidial pleurae.

**Variability.** The convexity of the carapace, mainly that of the pygidium, varies (Pl. 20, figs. 3, 4).

**Comparison.** From *X. devexus*, it differs in the highly elevated palpebral lobes, which are closer to the posterior margin of the cephalon, in the presence of the flexure between the frontal and medial lobes, and in the better developed occipital furrow.

**Occurrence.** Volkhov River, Valim Formation, lower part of the beds with *Xenasaphus*.

**Material.** Eighty-five specimens from the type locality.

### Genus *Delphasaphus* Ivantsov, 2000

*Xenasaphus* (*Delphasaphus*): Ivantsov, 2000, p. 55.

**Type species.** *Asaphus delphinus* Lawrow, 1856.

**Diagnosis.** Cephalon elongated; basal lobes present; eyes low; eye pedicles absent; palpebral lobes situated below level of middle part of glabella; genal corners rounded; narrow border developed in front of glabella; on cephalon, vincular apparatus represented by deep pits with slitlike opening on outer surface of shield; pygidium elongated, without bordering; rachis coarsely segmented, segments not interrupted on its axis; panderian organs neosaphine.

**Description.** The carapace is large, the maximum measured width of the cephalon is 50.3 mm. The cephalon is elongated (l/d specimen PIN, no. 4330/130, 0.6), anteriorly acuminate, without beaklike bend, with straightened lateral margins. The glabella is divided into a very large, rhomboid frontal lobe, small rectangular medial lobe, and basal lobes. The frontal lobe of the glabella is weakly convex, with the maximum convexity in the anterior part, not reaching the anterior margin, anteriorly bordered by a sharp furrow, lacking the longitudinal ridge. The medial lobe is distinctly bordered laterally, the flexure between it and the frontal lobe is absent. The basal lobes are lenslike and weakly expressed. Rudiments of the glabellar lobes are absent. The eyes are small, low, approaching the posterior margin, and widely separated. The palpebral lobes are situated lower than the glabella. The eye socles are underdeveloped. The eye lists are weakly expressed. The eye pedicles are absent. The ocular areas are not elevated above the cephalon, their posterior margins are devoid of ridges and tubercles. The anterior branches of the facial sutures run parallel and adjacent to the anterior margin along most of their length. The cranidium is

somewhat obtuse anteriorly. The distance between the facial sutures at the level of the marginal bends is greater than that at the level of the eye socles. The anterior part of the librigena is uniform in width. The occipital node is diffused. The fixed genae are convex and possess a narrow bordering starting from the anterior margins of the vincular pits. The genal corners are rounded. The paradoublural furrows are absent. The vincular pits are deep, expressed on the outer surface as narrow slitlike openings on the lateral margin. The occipital ring and rings of the body rachis are weakly convex. The pygidium is elongated (L/D, specimen PIN, no. 4330/132, 0.64), with the lateral margins being straightened and the acuminate posterior end. The rachis is broad, coarsely segmented, and weakly bordered posteriorly. The segments are not interrupted on the rachial axis, the number of visible segments is up to eight. The pleurae are convex, smooth, and lack bordering. The facets widen toward the lateral corners of the pygidium. The D-folds are rather coarse, they emphasize the segmentation on the anterior part of the frontal lobe of the glabella, anterior parts of the librigenae and fixed genae, and on the pygidial rachis and form radial and transverse folds on the pygidial pleurae. The panderian organs are neosaphine.

**Specific composition.** One species, *D. delphinus* (Lawrow, 1856).

**Comparison.** This genus is closest to the genus *Xenasaphus*, from which it differs in the slitlike openings of the vincular apparatus on the cephalon and in the absence of the border from the pygidium.

**Occurrence.** Baltic-Ladoga Glint; Middle Ordovician, Llanvirn, Aseri Horizon, the upper part of the beds with *A. intermedius*-*A. kowalewskii*.

### *Delphasaphus delphinus* (Lawrow, 1856)

Plate 19, figs. 1-4

*Asaphus delphinus*: Lawrow, 1856, p. 238, pl. 4, figs. a-c; Schmidt, 1901, p. 45, pl. 3, figs. 8-12; pl. 12, fig. 15, text-figs. 5, 33, and 34; Lesnikova and Weber, 1949, p. 282, pl. 72, figs. 2 and 3.

*Asaphus* (*Neosaphus*) *delphinus*: Jaanusson, 1953a, p. 398; Balashova, 1976, p. 17

*Asaphus* (*Trematophorus*) *delphinus*: Balashova, 1953, p. 404, pl. 1, figs. 12, 19; pl. 3, figs. 4 and 5.

*Xenasaphus* (*Delphasaphus*) *delphinus*: Ivantsov, 2000, pl. 9, fig. 4.

**Lectotype.** StPSMI, no. 56/6, designated by me (Ivantsov, 2000), unrolled carapace, village of Ropsha; stratigraphic position not detected (Pl. 19, fig. 4).

**Diagnosis.** As for the genus.

**Remarks.** The invalidity of the neotype designated by Balashova (1953) is discussed in the introductory part of Systematic Paleontology.

**Occurrence.** Middle Ordovician, Llanvirn, Aseri Horizon, upper part of the beds with *A. intermedius*-*A. kowalewskii*; upper part of the Duboviki Formation. Outside the Ladoga Glint: Baltic Glint (Schmidt, 1901).

**Material.** Twenty-five specimens: Volkhov River, 7.6–7.7 m above ds4 or 1.15–1.25 m below the floor of the Porogi Formation; Lava River, 1.25–1.35 m below the floor of the Porogi Formation.

### Genus *Onchometopus* F. Schmidt, 1898

*Asaphus (Onchometopus)*: Schmidt, 1898, p. 28; 1901, p. 82; Jaanusson, 1953a, p. 397; 1959, p. 336.

*Onchometopus*: Lamanskii, 1905, p. 64; Zittel, 1934, p. 951; Lesnikova and Weber, 1949, p. 278; Hupé, 1955, p. 200; Balashova, 1960, p. 144; 1976, p. 24.

**Type species.** *Asaphus (Onchometopus) volborthi* F. Schmidt, 1898.

**Diagnosis.** Cephalon with average proportions; glabella not divided into lobes; palpebral lobes lower than middle part of glabella; genal corners rounded; vincular apparatus represented by groove extending along entire anterolateral margin; pygidium shortened; panderian organs asaphine.

**Description.** The carapace is of medium size. The cephalon is elongated (mean l/d, 0.54), rounded anteriorly, with a sharp beaklike bend. The glabella is nearly cylindrical, weakly compressed between the eyes, and undivided into lobes; its frontal part is strongly convex, reaching and slightly overhanging the anterior margin, and lacking the longitudinal ridge. Rudiments of the glabellar lobes are absent. The eyes are medium-sized, closer to the anterior margin, and widely separated. The palpebral lobes are situated below the level of the middle part of the glabella. The eye socles are fully developed. The eye lists and pedicles are absent. The ocular areas are not elevated above the cephalon, their posterior margins are devoid of ridges and tubercles. The anterior branches of the facial sutures are developed as gentle arches. The cranidium is acuminate anteriorly and has no lingula. The distance between the facial sutures at the eye socles is slightly less than the maximum distance between them near the anterior margin of the shield. The anterior part of the fixed gena weakly widens toward the anterior margin. The dorsal furrows are very shallow and more or less noticeable in front of the eyes only. The glabellar furrows are absent. The occipital furrow is either absent or poorly defined. The posterior marginal furrows are shallow. The fossulae are unclear. The paradoublural furrows are absent. The occipital node is absent. The librigenae are convex. The genal corners are rounded. On the cephalon, the vincular apparatus is represented by a narrow furrow extending along the anterolateral margin of the shield and forming an abrupt fold beneath the glabella. The occipital ring is flat. The rings of the body rachis are narrow and strongly convex. The pygidium is shortened (mean L/D, 0.54), with rounded lateral margins. The rachis is broad, weakly segmented (four or five segments interrupted on the rachial axis are visible), and weakly bordered posteriorly. The pleurae are weakly convex and smooth and have no limbs. The facets widen toward the lateral corners of the pygidium. The D-folds are present on the anterior part of the glabella, the rings of the body rachis, and on the pygidial

rachis. The panderian organs are asaphine. When the carapace rolls up, the pleural margins of the body and pygidium are inserted into the groove on the doublure of the cephalon, and the posterior margin of the pygidium is set against the fold beneath the glabella (Pl. 19, fig. 6b).

**Specific composition.** One species, *Onchometopus volborthi* F. Schmidt, 1898.

**Comparison.** It differs from the other genera of the subfamily in the unsegmented glabella, weak development of the furrows on the cephalon, and in a distinctive type of vincular apparatus.

**Remarks.** The pygidium of trilobites belonging to this genus is typically asaphine. It is closest to pygidia of *A. expansus* and young *A. lepidurus* but differs from them in the more poorly expressed segmentation of the rachis and in the nearly complete absence of the terracelike folds from the outer surface. It differs from the pygidium of *A. ? broeggeri*, which occurs in association with it, in being shorter and in the stronger segmentation of the rachis.

**Occurrence.** Baltic–Ladoga Glint; Lower Ordovician, Arenig, Volkhov Horizon, beds with *A. ? broeggeri*.

### *Onchometopus volborthi* F. Schmidt, 1898

Plate 19, figs. 5 and 6

*Asaphus (Onchometopus) volborthi*: Schmidt, 1898, p. 28, figs. 3 and 4; Schmidt, 1901, p. 82, pl. 10, figs. 9–12, text-figs. 48–52; Lesnikova and Weber, 1949, pl. 72, figs. 6 and 7; Jaanusson, 1953a, p. 397.

*Onchometopus volborthi*: Lamanskii, 1905, p. 64; Balashova, 1976, p. 24.

**Lectotype.** PIN, no. 4248/12, unrolled carapace, depicted by Schmidt (1901, pl. 10, fig. 9), designated by Balashova (1976), status changed here; Volkhov River, village of Izvoz; stage B<sub>2</sub>.

**Diagnosis.** As for the genus.

**Remarks.** The type of the species was named a holotype by Balashova (1976), which is incorrect, because it had not been designated by the author and the type collection included several specimens.

**Occurrence.** Lower Ordovician, Arenig, Volkhov Horizon, beds with *A. ? broeggeri*; Volkhov Formation, Zheltyaki Member and the lower part of the Frizy Member. Outside the Ladoga Glint: Baltic Glint, Toila Formation, Künnapõhja Member.

**Material.** Forty-six specimens: Volkhov River, village of Babino, 0.3 m above the Dikari roof or 4.65 m below ds2; Lava River, Putilovo River, 1.9–2.1 m above the Dikari roof or 2.9–3 m below ds2.

### Asaphinae? gen. et sp. indet.

Plate 7, fig. 5

*Asaphus laevisimus* var. *laticauda*: Lesnikova and Weber, 1949, pl. 71, fig. 2.

**Description.** The pygidium is very large (D up to 100 mm), shortened, low, with rounded lateral mar-

gins and a rounded or slightly obtuse posterior end. The posterolateral margin is generally horizontal. The rachis is long, narrow, weakly separated from the pleurae, and weakly segmented (two or three segments are visible on its outer surface). The pleurae are flat and smooth and have no bordering. The facets are narrow and narrow even more toward the lateral corners of the shield.

**Comparison.** These shields resemble pygidia of *Subasaphus* in their large size, flattening, and in the smoothed relief but differs in the posterolateral margin being horizontal. The pygidia in question differ from all genera of Asaphinae in being narrow and narrowing toward the lateral corners of the shield facets.

**Remarks.** Apparently, finds of "large pygidia of *Asaphus laticaudatus*" in the middle part of the Duboviki Formation (Balashova and Balashov, 1961; Yanishevskii, 1931) are referred to this form.

**Occurrence.** Middle Ordovician, Llanvirn, Aseri Horizon, Duboviki Formation, beds with *A. intermedius*—*A. kowalewskii*.

**Material.** Eight pygidia: Volkhov River, 5–5.45 m above ds4 or 3.4–3.85 m below the floor of the Porogi Formation; Lava River, 3.5 m below the floor of the Porogi Formation.

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