The Ordovician trilobite genus *Robergia* Wiman, 1905 and some other species hitherto included

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The genus *Robergia* Wiman, 1905 is revised together with type and additional material including *R. striatella* sp. nov. from the upper Llandeilo/lower Caradoc of Jämtland, Sweden. This species is similar to both older and younger forms from North America, and 'European' and 'American' stocks are recognized. *Pugilator* gen. nov. is erected for late Ordovician species with short palpebral lobes and a large glabellar tongue, and *Arator* gen. nov. for species from Kazakhstan, U.S.S.R., with a narrow glabellar tongue and a falcate, prominent anterior border. Type material of *R. breviceps* Raymond, 1925 is illustrated for the first time and the species assigned to *Eorobergia*.

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On a visit to the Palaeontological Institute at the University of Uppsala in 1968 I received on loan from the late Professor Per Thorslund some excellent remopleuridid material from Jämtland, including that of an undescribed species of *Robergia*. It was agreed that this should be included with Norwegian material I was revising, but this was not done (Nikolaisen 1983). It is therefore described here to show how it throws important light on the understanding of the genus *Robergia*. In addition, study of comparative material has led to the erection of two new genera.

The terminology used follows that of Harrington et al. (1959, pp. *O*117–*O*126), Whittington (1959b, pp. 375–378) and Nikolaisen (1983, text-fig. 1), but 'palpebral rim' and 'dorsal furrow' have been substituted by 'palpebral lobe' and 'axial furrow', respectively. The term 'epipalpebral furrow' for the longitudinal furrow dividing the anterior and posterior palpebro-ocular ridges introduced by Cowie & McNamara (1978, p. 616; McNamara 1978, p. 636) is preferred to 'ocular furrow' (Sdzuy 1978, p. 93) and to 'palpebral ledge' Shergold 1972, op. 15). Lateral glabellar furrows are numbered S1–S3, as proposed by Jaanusson (1956, p. 37; also Henningsmoen 1957, pp. 154–157). Terms describing exuvial assemblages were proposed by Henningsmoen (1975, p. 182). Forms with posterior margin of palpebral lobes reaching and not reaching as far back as opposite the occipital furrow are referred to as 'remopleuridioid' and 'robergioid', respectively.

Stratigraphical correlations between Scandinavia, Great Britain, North America and Kazakhstan follow Jaanusson (1982), Jaanusson & Karis (1982), Whittington (1972), Tripp (1980), Barnes et al. (1981), Ross et al. (1982), Nikitin et al. (1968) and Nikitin (1972).

The figured specimens were coated with a dilute opaque, then lightly whitened with a sublimate of ammonium chloride before photographing, using the technique described by Whittington (1956).

Magnesian oxychloride replicas of figured type specimens from Kazakhstan have been made from 'Antogermetic' rubber paste casts using the method described by Stitt (1982). Illustrated cranidia are oriented with the palpebral lobes horizontal and referred to as 'dorsal view', unless otherwise stated.

The catalogue numbers of specimens are prefixed (or suffixed) as follows:

A	Hunterian Museum, Glasgow.
BM	The Natural History Museum, London.
GM IGN	Geological Museum of the Institute of Geological Sciences, Alma Ata, AN KazSSR.
GSC	Geological Survey of Canada, Ottawa, Canada.
LO	Department of Historical, Geology and Paleontology, Lund University, Sweden.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachussetts.
NIGP	Nanjing Institute of Geology and Palaeontology, Nanjing, China.
PMO	Paleontological Museum, University of Oslo.
SGU	Geological Survey of Sweden, Uppsala.
USNM	U.S. National Museum of Natural History, Washington, D.C.

Systematic descriptions

Genus *Robergia* Wiman, 1905

Type species. – *Remopleurides microphthalmus* Linnarsson, 1875, by monotypy, from the Andersö Shale at Önsvedsbäcken, Jämtland in Sweden.

Diagnosis. – A remopleuridid genus with length of broad (tr.) palpebral lobes (exsag.) almost half that of cranidium (sag.), extending from well in front of abaxial ends of S3 to well behind S1 and with an epipalpebral furrow.

General description. – A remopleuridid genus with: length of broad (tr.) palpebral lobes (exsag.) almost half that of cranidium (sag.), extending from well in front of abaxial ends of S3 to well behind S1, but with posterior margin not as far back as opposite occipital furrow, and with an epipalpebral furrow; glabella narrow posteriorly, expanding to nearly twice posterior width between palpebral lobes; glabellar tongue bulbous, as wide as or slightly wider than occipital ring but clearly narrower than and smaller than median area of glabella, and with strongly convex lateral margins; three pairs of lateral glabellar furrows present; anterior border usually very narrow (sag.) and rim-like; librigenae with very narrow (tr.) genal field, genal spines originating from opposite or slightly behind transversal mid-line of palpebral lobes causing deep genal notches; hypostome (where known) ellipsoid with large oval areas with prosopon of curved striae; thorax of eleven tergites (where known) with transversely directed pleurae lacking both fulcral processes and fulcral sockets, terminating in small backwardly directed spines, and with broad (exsag.) but shallow diagonal pleural furrows; pygidium with length about equal to width, axis extending more than half of sagittal length of pygidium, pleural fields flat but with three pairs of broad and shallow pleural furrows, and three pairs of marginal spines, the third pair may be expressed only as blunt rounded prolongations.

Remarks. – Whittington (1950, pp. 543–544, Pl. 71, figs. 1–6, 8, *non* fig. 7) redescribed the type species but gave no diagnosis. The later diagnosis (Whittington 1959a, pp. *O*327–*O*328) was based on the then incompletely known type and other species from North America illustrating one (Whittington 1959a, Fig. 241/3) which is not thought to belong to *Robergia*. Features of the thoracic tergites are based on new Swedish material of the type species, including a nearly complete exoskeleton in moulting position (see Nikolaisen 1983, Pl. 15, fig. 8; this paper Fig. 13E).

Ross & Shaw (1972, pp. 16–17) have remarked on how similar cranidia of *Robergia* species are. Even the pattern of the prosopon on the median area of the glabella may be nearly identical (cf. e.g. *R. schlotheimi* in Whittington 1965, Pl. 40, fig. 12 and *R. striatella*, Fig. 15G herein). Nevertheless, well-preserved specimens may be specifically separated on other but minor characters such as the strength of the median furrow and relative length of the glabellar tongue. With the exception of those species described by Koroleva (1965, 1982) *Robergia* species can be separated into two distinct groups based on the palpebral lobes. *Robergia* s.s. from the lower Llanvirn to lower Caradoc (but from Ashgill in China) includes species with long palpebral lobes extending from well in front of the abaxial ends of S3 to well behind S1 and a median area of glabella that is larger than the glabellar tongue. Included are: *R. microphthalma* (Linnarsson, 1875), *R. barrandii* (Etheridge & Nicholson, 1879), *R. major* Raymond, 1920 (including *R. athenia* Butts, 1926), *R. scanica* Hadding, 1913, *R. schlotheimi* (Billings, 1865), *R. sinensis* Lu & Chang, 1974, *R. sparsa* Nikolaisen, 1983 and *R. striatella* sp. nov. Additionally, *Robergia* sp. nov. (determination by Apollonov) is listed by Nazarov & Popov (1980, p. 9) from the Tselinograd horizon, Bestamiak Formation at Chagan, Sargaldek, Konyr-auliy, Kazakhstan. *Pugilator* gen. nov. from the middle Caradoc to the Ashgill has short palpebral lobes extending from behind the abaxial ends of S3 to opposite or slightly behind S1 and a median area of glabella that is smaller than the glabellar tongue (cf. Figs. 8–9). Species included here are *P. yukonensis* (Churkin, 1966), *P. deckeri* (Cooper, 1953) and *P.* sp. (cf. Chugaeva 1964, p. 29, Pl. 1, fig. 12). This is in agreement with a previous view by Whittington (pers. comm. in Lenz & Churkin 1966, p. 44).

Pygidia of *Robergia* are interspecifically much more variable than the rest of the dorsal exoskeleton, but appear to be intraspecifically stable and thus the exoskeletal part on which reliable diagnostic characters can best be based.

The sagittal furrow occurring between S3, as in *R. striatella* (cf. p. 58, Fig. 15C), has been reported in *Pugilator yukonensis* by Churkin (1966, p. 41, Pl. 4, Pl. 5, figs. 1–5) and in *R. sparsa* by Nikolaisen (1983, pp. 293–294, Pl. 15, figs. 2, 4). However, such a feature is not as rare as believed and previous authors have most probably misinterpreted the furrow as being of secondary origin, i.e. accentuated by crushing (cf. Ross & Shaw 1972, pp. 15–16). It is present in *R. barrandii* (see Reed 1903, Pl. 5, fig. 1; Tripp 1980, Pl. 3, fig. 18), *R. major* (see *R. athenia* Cooper, 1953, Pl. 12, fig. 13; Whittington 1959b, Pl. 18, fig. 5; Ross & Shaw 1972, Pl. 1, figs 16–17, 20), *R. schlotheimi* (see Whittington 1965, Pl. 41, figs. 5, 8) and *Pugilator deckeri* (see Cooper 1953, Pl. 2, fig. 5), and in *Arator* gen. nov. (cf. Fig. 16A–B).

Robergia microphthalma (Linnarsson, 1875)

Figs. 1a–d; 13A–I; 14A–I

1872 hufvud af en [head of a] *Remopleurides* – Linnarsson, p. 41 (recorded).

1872 pygidier af en [pygidia of a] *Dikelocephalus* – Linnarsson, p. 41 (recorded).

1875 *Remopleurides microphthalmus* n. sp. – Linnarsson, pp. 494–495, Pl. 22, fig. 3 (descr. and fig. of cranidium).

1894 *Remopleurides microphthalmus* Lns. – Wiman, p. 267 (listed).

1897 *Remopleurides microphthalmus* Linrs. – Holm, pp. 464–467, Pl. 8, figs. 1–2 (descr., remarks and figs. of librigenae and pygidium).

1898 *Remopleurides microphthalmus* Linrs. – Holm, pp. 18–21, Pl. 1, figs. 1–2 (same as Holm 1897).

1905 *Robergia microphthalma* Lns. – Wiman, pp. 77–78, Pl. 5, figs. 1–4 (remarks and figs of cranidia and pygidia).

non 1907 *Robergia microphthalma* Linrs. sp. – Moberg, pp. 83–87, Pl. 1, fig. 4 (remarks and fig. of cranidium) [= *R. scanica*].

1913 *Robergia microphthalma* Linrs. sp. – Hadding, p. 78, Pl. 8, figs. 15–17 (remarks and figs. of cranidia and pygidium).

non 1913 *Robergia microphthalma*? Linrs. sp. – Hadding, p. 78, Pl. 8, fig. 18 (remarks and fig. of pygidium) [= *R. sparsa*].

1950 *Robergia microphthalmus* [sic] (Linnarsson, 1875) – Whittington, pp. 543–544, Pl. 71, figs. 1–6, 8 (descr. and figs. of holotype, librigenae of Holm 1897, and cranidium and pygidium of Wiman 1905).

non 1950 *Robergia microphthalmus* [sic] (Linnarsson) [partim.] – Whittington, pp. 543–544, Pl. 71, fig. 7 only (remarks and fig. of pygidium in Hadding 1913) [= *R. sparsa*].

1953 *Robergia microphthalma* – Størmer, p. 109 (listed).

1960b *Robergia microphthalmus* [sic] (Linnarsson) – Kobayashi, Fig. 3c (restorations of cephalon and pygidium).

1963 *Robergia microphthalma* – Skjeseth, pp. 72, 74 (listed).

1982 *Robergia microphthalma* (Linnarsson) – Karis, p. 58 (listed).

1983 *Robergia microphthalma* (Linnarsson, 1875) – Nikolaisen, pp. 294–295, Pl. 15, figs. 8–14 (remarks and figs. of exoskeleton, cranidia, thoracic tergite and pygidia).

1985 *Robergia microphthalma* (Linn.) – Kolobova, p. 168 (listed).

Holotype (by monotypy). – An incomplete, longitudinally compressed cranidium SGU type 3952 (labels accompanying the specimen are numbered 3953) from the Andersö ('Ogygiocaris') Shale, most probably the Zone of *Hustedograptus teretiusculus* or lowermost part of the Zone of *Nemagraptus gracilis* at Önsvedsbäcken, Jämtland in Sweden, figured by Linnarsson 1875, Pl. 22, fig. 3; also Whittington 1950, Pl. 71, fig. 6 and herein Fig. 13B.

Remarks. – The specimen in moulting position figured by Nikolaisen (1983, Pl. 15, fig. 8) shows at least ten thoracic

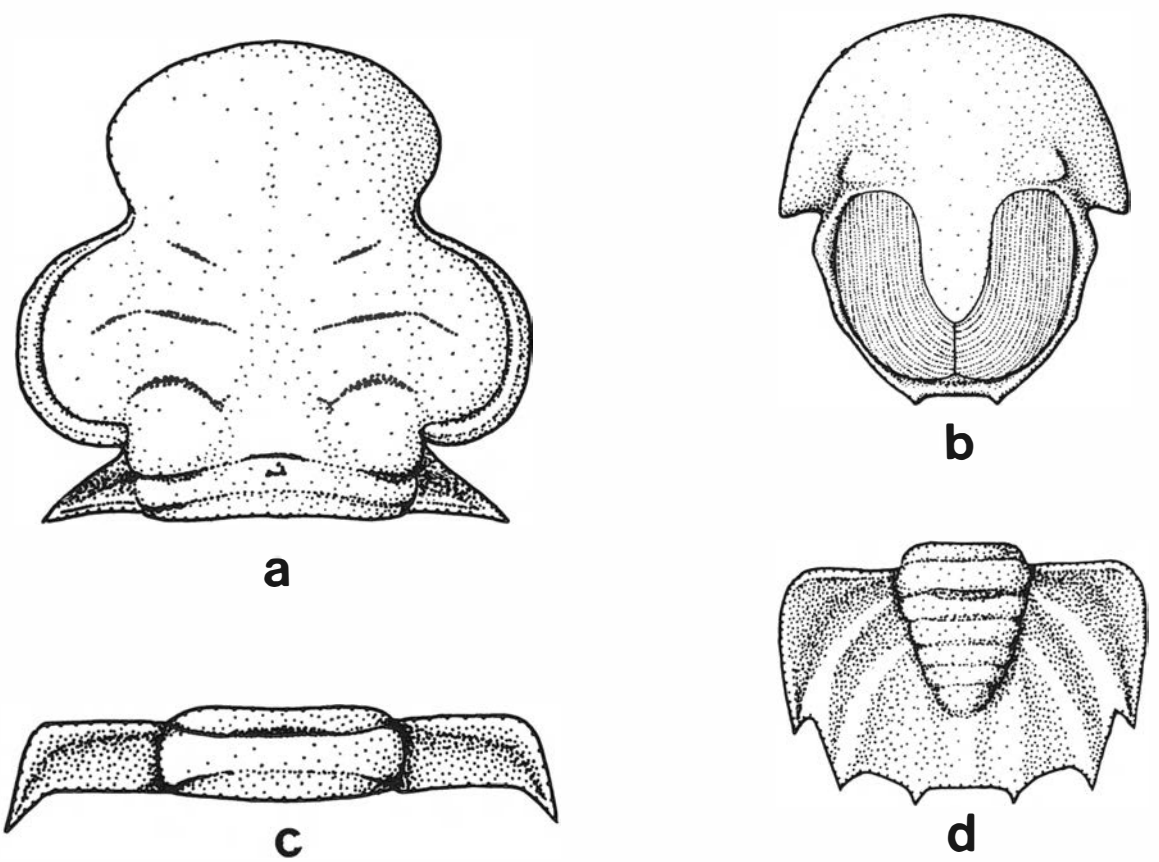

Fig. 1. Restorations of *Robergia microphthalma* (Linnarsson, 1875). Prosopon omitted. a. Cranidium based on Fig. 13E, H–I, the original of Wiman, 1905, Pl. 5, fig. 2, and Whittington 1950, Pl. 71, figs. 2–4. b. Hypostome based on Figs. 13E–F and 14H. c. Thoracic tergite based on topotype material and Nikolaisen 1983, Pl. 15, fig. 14. d. Pygidium based on Figs. 13E and 14I and Nikolaisen 1983, Pl. 15, figs. 12–13.

tergites, but fragments of an eleventh seem to be present, the same number as in *R. major* and the probably synonymous *R. athenia* (see Cooper 1953, Pl. 8, fig. 11, Pl. 12, fig. 13). The thoracic tergites have an axial ring which is more than twice as wide (tr.) as that of each pleura between axial furrow and fulcral line and carry a well marked and strong articulating furrow. The flat pleura has a diagonal furrow, lacks both fulcral processes and fulcral sockets and terminates in a short but acute, triangular and backwardly directed spine.The doublure outside the fulcral line is triangular and striated. The prosopon pattern on the axial ring of isolated tergites is similar to that on the occipital ring (cf. Fig. 14A–B). To the upper left of the specimen (Fig. 13E–F) are the librigenae with the hypostome in between (Fig. 13E–F). Unfortunately they are compressed laterally and vertically. A slightly better and more complete hypostome (Fig. 14H) occurs on the same piece of rock as Holm's illustrated specimens (1897, Pl. 1, figs. 1–2). It is oval in outline, only very slightly longer than wide. The anterior lobe is almost half as long as the entire hypostome, strongly convex both longitudinally and transversally, and with the large anterior wings located behind the transversal mid-line. The posterior lobe is defined laterally and posteriorly by a well-marked and strongly convex (ventral view) border. The two oval areas are reniform, separated posteriorly by a very fine sagittal furrow (the large connected posterior part on the hypostome in Fig. 13E–F is accentuated by exaggerated preparation) and with distinct and parallel striae. A pair of gently raised but conspicuous bulges are present just in front of the oval areas. The prosopon on the anterior lobe consists of low, anastomozing ridges. The rarity and fragmentary preservation of hypostomes suggests that they were originally thin. The hypostome of *R. microphthalma* is similar to that of *R. schlotheimi* (see Whittington 1965, p. 376, Pl. 41, figs. 3–4, 7), but from which it differs mainly in having a shorter anterior lobe, a pair of anterolateral bulges and in having the oval areas separated posteriorly only by a very fine furrow. Thus the hypostomes of these two species differ considerably from both *R. major* (see Whittington 1959b, Pl. 18, figs. 9–14) and *R. barrandii* (see Tripp 1980, Fig. 3h, Pl. 1, fig. 7), which are more like those of *Remopleurides*. Hypostomes of other species of *Robergia* are as yet unknown.

Many external moulds show a dense and very fine cranidial prosopon (Fig. 14A–B), as in *R. schlotheimi* or *R. striatella*, but differ, however, in being transverse between anterior tips of the palpebral lobes. Also, the striae on the palpebral lobes in *R. microphthalma* differ in not being subparallel to the margins, but curving outwards and forwards (Fig. 14B).

Some poorly preserved ontogenetic stages from the Zone of *Glyptograptus teretiusculus* at Högen, Sunne Sokn in Jämtland are figured (Fig. 14D–G), but they add very little to our knowledge of the ontogeny in remopleuridid trilobites.

The Jämtland material includes at least three moulting assemblages (Figs. 13E, G; 14A) in which the position of the librigenae in relation to the cranidium (or the hypostome) is different. They are parallel, right side up and not rotated in the complete exoskeleton (Fig. 13E), whereas in the two upper cephalic units the left librigena is rotated approximately 90° clockwise and the right librigena about 180° so (Figs. 13G, 14A). In the case of the latter both librigenae are right side up, whereas in the former the left cheek is inverted. The most likely interpretation of these positions is that the trilobite firstly raised its head upward in an almost vertical position so that the genal spines pointed to the bottom, then twisted it backwards and forwards. Presumably the released librigenae would fall to the sediment surface more or less at random due to currents made by the movement of the head. Further information concerning the type species is given below. It should, however, be added here that the type species has been collected by P. Thorslund and by B. Asklund from both the Zone of *Hustedograptus teretiusculus* and the Zone of *Nemagraptus gracilis* in the Andersö Shale in Jämtland. Karis (1982, p. 58) also lists *R. microphthalmus* from both zones. Thus, as noted by Hadding (1913, pp. 28, 89), the type species has a range spanning at least parts of two graptolite zones. It occurs also fairly commonly in the Hovindsholm Shale in the northern districts of the Oslo Region (Nikolaisen 1983, p. 295), which mainly corresponds to the Zone of *Nemagraptus gracilis* (Bruton, pers. comm., July, 1990).

Occurrence. – Sweden: Andersö Shale, Zone of *Hustedograptus teretiusculus* and lower part of Zone of *Nemagraptus gracilis*. Önsvedsbäcken, Andersön, northern Norderön, northeast side of Frösön and Högen, all in Jämtland. Norway: Hovinsholm Formation ('Robergia Beds'), mainly the Zone of *Nemagraptus gracilis* (D. L. Bruton, pers. comm., July 1990). Heramb and Holmen in Ringsaker. (Størmer 1953, p. 103, lists the species from the 'Cephalopod Shale' [= upper part of the Hovinsholm Formation] at the western shore of Helgøya in the Nes–Hamar district, but I have not been able to trace the material.) U.S.S.R. (listed by Kolobova 1985): Tselinograd horizon, most probably Zone of *Nemagraptus gracilis*. Southwest of Lake Alakol, southwest Pribalkhash, Kazakhstan.

Robergia barrandii (Etheridge & Nicholson, 1879)

Figs. 2a–b, 14L–N, 15A–B

1879 *Remopleurides (Caphyra) Barrandii*, Eth. jun., and Nich., *(sp. nov.)* [partim.] – Nicholson & Etheridge, pp. 151–153, Pl. 10, fig. 13 only (descr. and fig. of cranidium), *non* Pl. 10, figs. 14–15, Pl. 11, fig. 16 [= *Robergiella* spp.].

1879 *Cheirurus* (?) sp. ind. (a.) – Nicholson & Etheridge, p. 203, Pl. 14, fig. 11 (short descr. and fig. of pygidium).

?1899 *Remopleurides Barrandei* [sic] (Eth. & Nich.) – Peach & Horne, pp. 509, 514, 673, 698, 702 (listed).

1903 *Apatokephalus*, sp. – Reed, pp. 30–31, Pl. 4, fig. 9 (descr. and fig. of Nicholson & Etheridge's original of *Cheirurus* (?) sp. ind. (a)).

1903 *Remopleurides barrandei* [sic], Nicholson & Etheridge, 1879 – Reed, pp. 31–33, Pl. 5, figs. 1–4 (descr., selection and fig. of holotype and figs. of add. cranidia).

1931 *Robergia barrandei* [sic] (Etheridge & Nicholson) – Reed, pp. 7–8 (remarks and transfer of *Apatokephalus* sp.).

1953 *Apatokephalus* sp. indet. by Reed, 1903 – Kobayashi, p. 52 (suggests the specimen figured by Reed transferred to *Robergia*).

non 1959 *Robergia barrandei* [sic] (Etheridge et Nicholson), 1879 – Balashova, pp. 25–26, Pl. 1, figs. 18–19 (descr. and figs. of cranidia) [= *Arator* sp.].

non 1960 *Robergia barrandei* [sic] (Etheridge et Nicholson), 1879 – Balashova, pp. 25–26, Pl. 1, figs. 18–19 (copy of Balashova 1959).

1980 *Robergia barrandii* (Etheridge & Nicholson) – Tripp, Fig. 3h, Pl. 1, figs. 26–28, Pl. 3, fig. 18 (figs. of meraspid cranidium, holaspid cranidium, hypostome and pygidium).

Holotype (selected by Reed 1903). – A cranidium, BM In. 21004, from the Lower Ardmillan Series, Balclatchie Group at Balclatchie, Girvan, Ayrshire, Scotland, figured by Etheridge & Nicholson 1879, Pl. 10, fig. 13; also Reed 1903, Pl. 5, fig. 1 and herein Fig. 15B.

Remarks. – The cranidium and pygidium were well described by Etheridge & Nicholson (1879) and Reed (1903), though it should be added that the epipalpebral furrow is not obvious and there is a narrow (exsag.) and convex (exsag.) anterior border which laterally exceeds for a short distance the glabellar tongue (Fig. 15A). As pointed out by Reed (1903, p. 32), the strong cranidial prosopon is a diagnostic feature. On the palpebral lobes it consists of strong furrows running subparallel to the margins, and it is possible that one of them on each lobe actually represents the epipalpebral furrow. Other than the holotype, thus the specimens figured by Etheridge & Nicholson are in error (Reed 1903, p. 32). The cranidia (Etheridge & Nicholson 1879, Pl. 10, figs. 14–15) belong most probably to *Robergiella* spp., the cephalon (loc. cit., Pl. 10, fig. 16) is the type specimen of *Remopleurides* [= *Robergiella*] *correctus* Reed (1903, pp. 37–38, Pl. 6, figs. 1–3, *non* figs. 4–5) and the cranidium (Etheridge & Nicholson 1879, Pl. 11, fig. 16) was illustrated as *Robergiella* sp. by Tripp (1980, Pl. 1, fig. 29). Three pygidia were briefly described by Etheridge & Nicholson, one of which (loc. cit., Pl. 14, fig. 11) was assigned to *Cheirurus* (?) sp. ind. (a) but was later (Reed 1903, pp. 30–31, Pl. 4, fig. 9) assigned to *Apatokephalus* sp. and thereafter (Reed 1931, p. 8) to *Robergia*. A small pygidium was figured by Tripp (1980, Pl. 1, fig. 28) and both the illustrated pygidia are refigured herein (Fig. 14M–N). The hypostome was figured by Tripp (1980, Fig. 3h, Pl. 1, fig. 27) and this resembles that of *R. major* (see Whittington 1959b, p. 429, Pl. 18, figs. 8–14). As yet, both the librigenae and the thorax remain unknown.

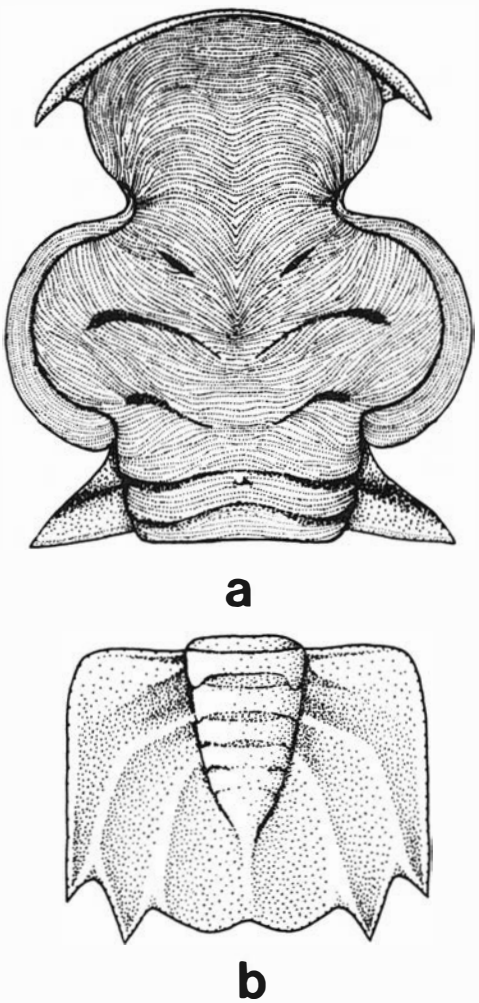

Fig. 2. Restorations of *Robergia barrandii* (Etheridge & Nicholson, 1879). a. Cranidium based on Fig. 15A and the holotype. b. Pygidium based on Fig. 14N–M and on several topotype specimens in BM (Natural History).

Occurrence. – Lower and upper Balclatchie Group and lower Ardwell Group, Girvan, Ayrshire, southwest Scotland.

Robergia major Raymond, 1920

Fig. 3a–b

1920a *Robergia* sp. – Raymond, p. 145, fig. 40 (drawing of restored dorsal exoskeleton).

1920b *Robergia major*, sp. nov. – Raymond, pp. 281–282 (descr.).

1925 *Robergia major* Raymond – Raymond, pp. 60–61, Pl. 3, figs. 6–8, 10, *non* fig. 9 [= *Eorobergia*] (repeat descr. from 1920 and figs. of cranidium, librigena, thorax and pygidium).

1926 *Robergia athenia*, n. sp. – Butts, Pl. 19, figs. 3–6 (figs. of cranidium, thorax and pygidium).

1926 *Robergia major*, Raymond – Butts, Pl. 19, figs. 7–8 (figs. of cranidium and pygidium).

non 1933 *Robergia athenia* Ulrich [sic] – Decker, pp. 1415, 1419, 1422, 1424–1425, 1434 (recorded and remarks) [= *P. deckeri*].

1941 *Robergia major* Raymond – Butts, Pl. 82, figs. 4–7 (figs. of dorsal exoskeleton with shedded librigenae, thoracopygon and pygidia).

1953 *Robergia athenia* Butts – Cooper, p. 22, Pl. 12, figs. 10–14 (descr. and figs. of dorsal exoskeleton with shedded librigenae, cranidium and pygidia).

1953 *Robergia major* Raymond – Cooper, pp. 22–23, Pl. 8, figs. 7–11 (descr. and figs. of dorsal exoskeleton with shedded librigenae, cranidia and pygidia).

1959b *Robergia major* Raymond, 1920 – Whittington, pp. 428–431, Pl. 18, figs. 1–22, 25 (descr. and figs. of cranidia, librigenae, hypostomes and pygidia).

?*non* 1972 *Robergia major* Raymond, 1920 – Ross & Shaw, pp. 16–17, Pl. 1, figs. 8–15 (remarks and figs. of cranidia and pygidia) [? = *R.* sp. nov.].

Type specimens. – Syntypes are the specimens, M.C.Z. 1601–1606, from the lower part of the 'Athens' formation in the old quarry of Mathieson Alkali Works, about 3 km southeast of Saltville, Smyth County, Virginia, U.S.A., described by Raymond 1920b and figured 1925, Pl. 3, figs. 6–8, 10.

Remarks. – *R. major* seems to be common in the platform deposits ('Liberty Hall facies') of eastern North America (Cooper 1953; Whittington 1959b). The species was reported from the Caesar Canyon Limestone (equal to upper part of the Copenhagen Limestone) in Nevada by Ross & Shaw (1972, pp. 16–17, Pl. 1, figs. 8–15), but their figured specimens are different from topotype material. The glabellar tongue is as wide as and almost as long as the median area of the glabella, the palpebral lobes are shorter, the lateral glabellar furrows do not cross a corde between anterior and posterior ends of the palpebral lobes, and the pygidium does not taper in width backwards. Most likely the form from Nevada represents a separate species.

Occurrence. – Lower to middle(?) Caradoc off platform deposits ('Liberty Hall facies') of eastern North America, possibly but not likely also Caesar Canyon Limestone of Nevada, central U.S.A.

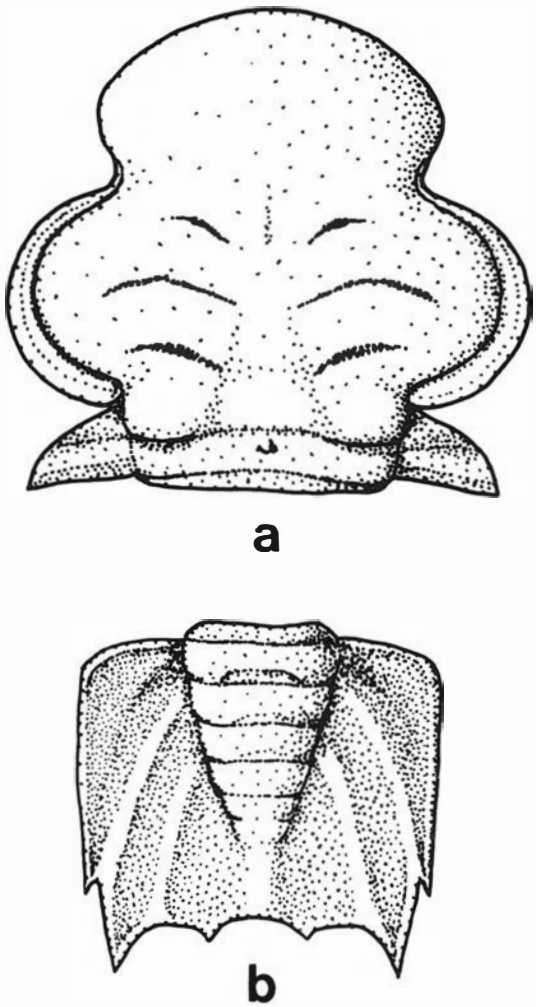

Fig. 3. Restorations of *Robergia major* Raymond, 1920. a. Cranidium based on Cooper 1953, Pl. 8, figs. 8, 10–11; Whittington 1959, Pl. 18, figs. 1, 3–6. b. Pygidium based on Cooper 1953, Pl. 8, figs. 7, 9; Whittington 1959, Pl. 18, figs. 22, 25. Prosopon omitted.

Robergia scanica Hadding, 1913

Figs. 5, 14J

1906 *Robergia microphthalma* Linrs *sp.* – Olin, p. 23 (recorded).

1907 *Robergia microphthalma* Linrs. sp. – Moberg, pp. 83–87, Pl. 1, fig. 4 (descr. and fig. of cranidium).

1913 *Robergia microphthalma* Linrs. var. *scanica* n. var. – Hadding, p. 70, Pl. 8, fig. 19 (short comparison with the nominate form and copy of Moberg's fig.).

Holotype (by monotypy). – The cranidium, LO 1997 t, from the Lower Dicellograptus Shale (most probably the Zone of *Hustedograptus teretiusculus*) at Röstånga, central Scania, Sweden, figured by Moberg 1907, Pl. 1, fig. 4; also Hadding 1913, Pl. 8, fig. 19 and herein Fig. 14J.

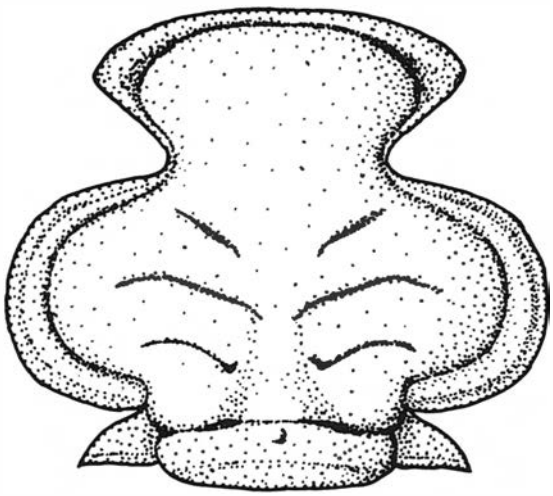

Fig. 4. Restoration of *Robergia scanica* Hadding, 1913. Based on the holotype, Fig. 14J. Prosopon omitted.

Diagnosis. – A *Robergia* with a slightly convex (exsag.) but distinct anterior border, glabellar tongue short (sag.) and slightly more than half as wide as median area of glabella, and with broad (tr.) palpebral lobes.

Remarks. – This form was originally described by Hadding as a variety of *R. microphthalma*, but the cranidium is so different that it should be regarded as a species (Raymond (1925, p. 63) referred to it as such without comment). It differs from *R. microphthalma* in having a broad (exsag.) and slightly convex (exsag.) anterior border, a considerably smaller glabellar tongue, apparently stronger lateral glabellar furrows and much broader (tr.) palpebral lobes with a broad but shallow epipalpebral furrow. In *Robergia*, a broad (sag., exsag.) preglabellar area is usually present only in immature individuals (cf. Cooper 1953, Pl. 12, fig. 1; Whittington 1959b, Pl. 18, figs. 16–17, 21). Thus the presence of such in the adult(?) cranidium of *R. scanica* may perhaps best be regarded as a case of arrested development (partial neoteny). However, only the holotype is known, and it may turn out that it really is from a juvenile individual. If so, *R. scanica* may have been of considerable size when fully grown.

Occurrence. – As for type specimen.

Robergia schlotheimi (Billings, 1865)

Fig. 5a–b

1865 *Remopleurides*(?) *Schlotheimi* n. sp. – Billings, p. 294, Fig. 284a–b (descr. and figs. of cranidia).

1897 *Apatokephalus Schlotheimi*, Billings – Brøgger, p. 184, Fig. 8a–b (transfer to *Apatokephalus* and copies of Billings' figs.).

1925 *Robergia schlotheimi* (Billings) – Raymond, pp. 58–60 (remarks).

1965 *Robergia schlotheimi* (Billings, 1865) – Whittington, pp. 375–377, Pl. 40, figs. 9–12, Pl. 41 (descr., selection and figs. of lectotype, paralectotypes, and topotype cranidia, hypostomes and pygidia).

Type specimen. – Lectotype, selected by Whittington 1965, a cranidium (GSC 694) from middle Table Head Formation at Pistolet Bay, western Newfoundland, figured by Billings 1865 Fig. 284a; also Whittington 1965, Pl. 41, fig. 1.

Remarks. – The pygidium of material from Nevada (see Ross & Shaw 1972, pp. 16–17, Pl. 1, fig. 15) is remarkably similar to that of *R. schlotheimi* and it only differs from this species and from *R. striatella* in possessing a shorter second pair of marginal spines. The cranidium (Ross & Shaw 1972, Pl, 1, figs. 8–14) differs from both *R. schlotheimi* and *R. striatella* in having a larger glabellar

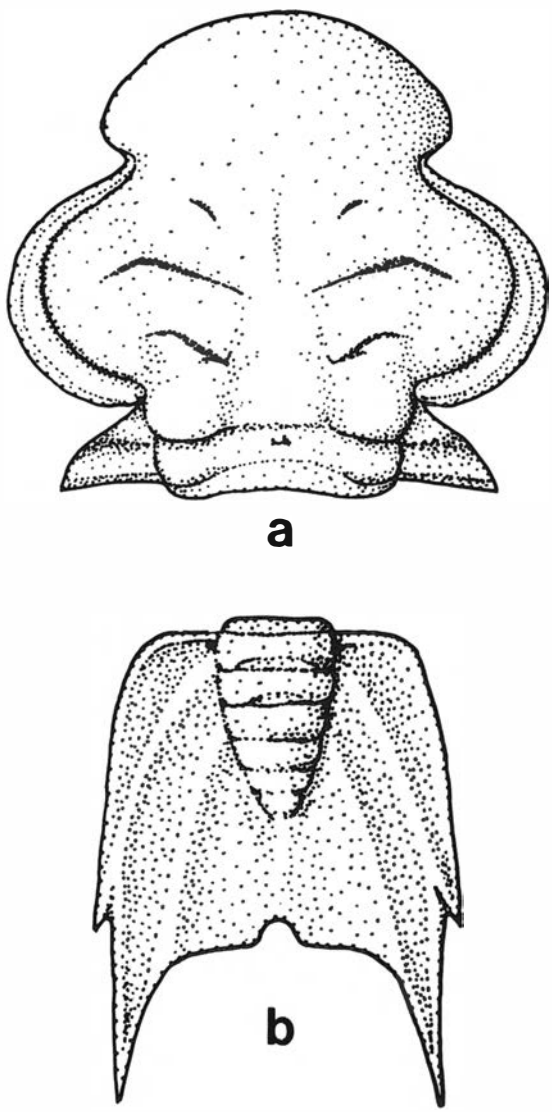

Fig. 5. a–b. Restorations of cranidium and pygidium of *Robergia schlotheimi* (Billings, 1865) based on Whittington 1965, pl. 40, figs. 10–12, Pl. 41, figs. 2, 9–10. Prosopon omitted.

tongue, shorter palpebral lobes, and lateral glabellar furrows not crossing a corde between the anterior and posterior ends of the palpebral lobe. The Nevada material may represent a separate 'off-shoot' derived from *R. striatella* or perhaps from *R. schlotheimi* and which migrated into the Central Basin during its submerge.

Occurrence. – Middle Table Head Formation and Middle Head Formation boulders in Cow Head Group conglomerates: various localities in western Newfoundland. Athens Shale (lower part): Saltville, Catawba Valley in Virginia.

Robergia sinensis Lu & Chang, 1974

Fig. 6a–b

1974 *Robergia sinensis* (sp. nov.) – Lu & Chang, p. 134, Pl. 55, figs. 5–6 (descr. and figs. of cranidium and pygidium).
1978 *Robergia sinensis* Lu – Yin, p. 520, Pl. 162, figs. 6–7 (repetition of Lu & Chang's descr. and figs.).
1986 *Robergia sinensis* – Chen & Qiu, p. 9 (listed).

Type specimens. – Lectotype (here selected) is the pygidium, NIGP 21555, from the middle Ashgill Wufeng Formation at Shihtzupu, Zunyi in the Guizhou Province, southwest China, figured by Lu & Chang 1974, Pl. 55, fig. 6; also Yin 1978, Pl. 162, fig. 7.

Description (translated from Lu & Chang 1974). – Cranidium widest across mid-length of palpebral lobes. Glabellar tongue broad. Three pairs of lateral glabellar furrows, of which the anterior pair is strongly oblique and forming an angle of 45° with the sagittal line, the median pair curved, and the posterior pair relatively deep and short. A pair of slightly convex and circular basal glabellar lobes present. Length of palpebral lobes slightly shorter than half the glabellar length, with their posterior ends separated from the occipital ring by the posterolateral limbs. Narrow anterior border in front of the anterior lobe of glabella. Anterior sections of facial sutures divergent. Occipital furrow deepening towards distal ends. Pygidium quadratic in outline, with a conical axis with five axial rings, pleural regions with three somites and with shallow pleural and interpleural furrows, and with three pairs of pygidial spines of which the second pair is large and long.

Remarks. – The cranidium of this late species is remarkably similar to that of the type species, *R. microphthalma*, and differs only in having slightly wider (tr.) palpebral lobes. The pygidium, however, has narrow (tr.) pleural fields with oblique anterior margins and strong, acute marginal spines of which the second pair is somewhat larger than the others. The pygidium is therefore diagnostic and differs from that of all other species. Therefore the pygidium is preferred as lectotype.

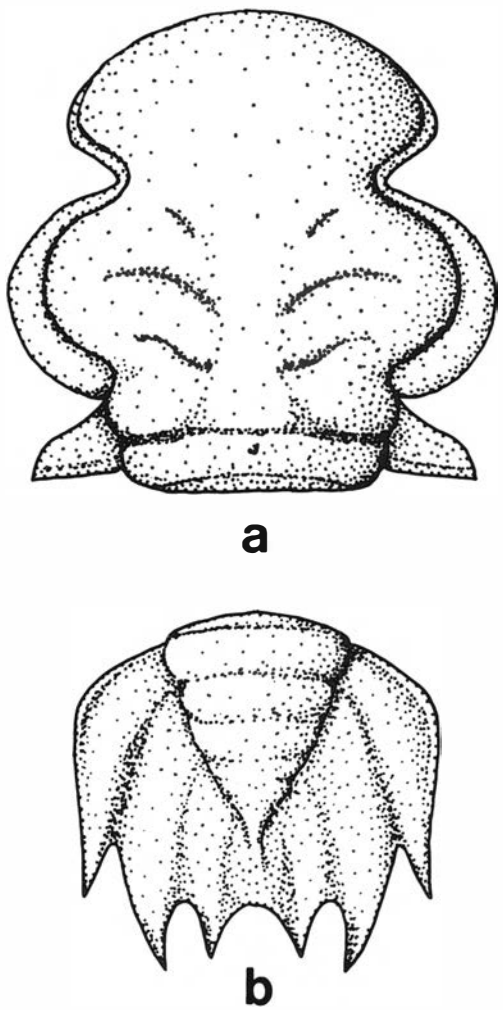

Fig. 6. a–b. Restorations of cranidium and pygidium of *Robergia sinensis* Lu & Chang, 1974. Based on syntypes figured by Lu & Chang 1974, Pl. 55, figs. 5–6; also Yin 1978, Pl. 162, figs. 6–7.

The pygidium of *R. major* (= *R. athenia*) illustrated by Butts (1926, Pl. 19, fig. 4), the small pygidium figured by Cooper (1953, Pl. 12, fig. 10) and the small pygidia figured by Whittington (1959b, Pl. 18, figs. 15, 19) all have a similar arrangement of the marginal spines as in *R. sinensis*. This may indicate that the latter is derived from the 'American' evolutionary stock (see below).

Occurrence. – Middle Ashgill Wufeng Formation. Shihtzupu, Zunyi, Guizhou Province, southwest China. Also listed (Chen & Qiu 1986) from Wufeng Formation, Yichang area, western Hubei Province, south China.

Robergia sparsa Nikolaisen, 1983

Figs. 7a–b, 14K

1913 *Robergia microphthalma*? Linrs. sp. – Hadding, p. 78, Pl. 8, fig. 18 (remarks and fig. of pygidium).
1950 *Robergia microphthalmus* (Linnarsson, 1875) [partim] – Whittington, pp. 543–544, Pl. 71, fig. 7 only (fig. of Hadding's pygidium).

1953 *Robergia microphthalma* – Størmer, p. 58 (listed).
1983 *Robergia sparsa* n. sp. – Nikolaisen, pp. 292–294, Pl. 15, figs. 2–7 (descr. and figs. of cranidia and pygidia).

Holotype. – A cranidium (PMO 75055) from the Elnes Formation ('Ogygiocaris Shale') at Furnes, Nes–Hamar district, Norway, figured by Nikolaisen 1983, Pl. 15, figs. 2–3.

Remarks. – Hadding (1913, p. 78) referred the pygidium (ibid., Pl. 8, fig. 18; herein Fig. 14K) with doubt to *R. microphthalma*, but did point out how it differed from the other pygidia in his material, concluding that its aberrant shape was due to deformation in the shale. Both the gross morphology and the pattern of the prosopon agree very well with that of *R. sparsa* and for which reason it is included here.

Occurrence. – Elnes Formation ('Ogygiocaris Shale'), Norway: Furnes in the Nes–Hamar district, Dambo and Slemmestad in the Oslo–Asker district. Andersö ('Ogygiocaris') Shale, Sweden: Andersö, Sunne in Jämtland, Sweden.

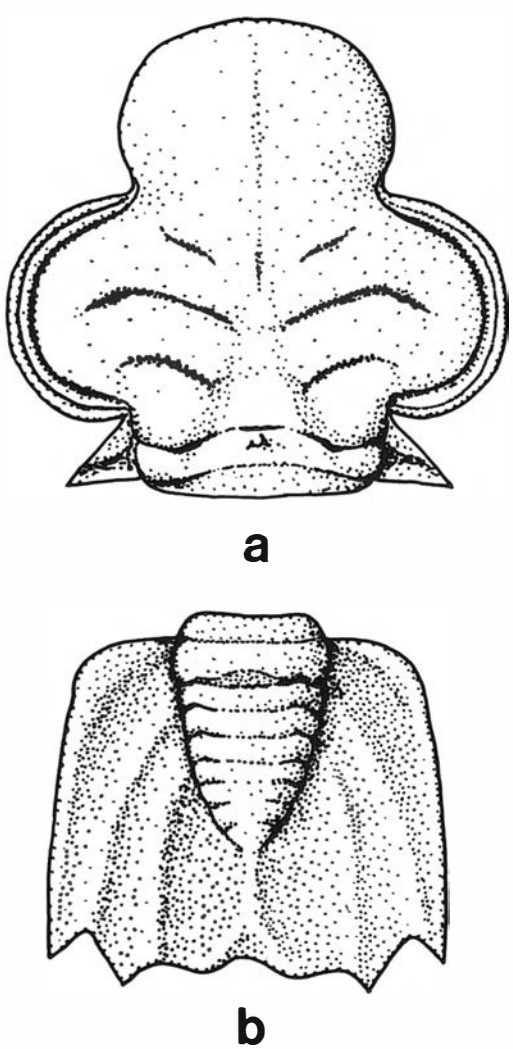

Fig. 7. a–b. Restorations of cranidium and pygidium of *Robergia sparsa* Nikolaisen, 1983, based on Nikolaisen 1983, Pl. 15, figs. 2–7. Prosopon omitted.

***Robergia striatella* sp. nov.**

Fig. 15C–H

1937 *Robergia* n. sp. – Thorslund, p. 11 (reported).

Name. – Diminutive of Latin *striatus*, hollow out, channel, groove, furrow, flute, alluding to the very fine and closely spaced striae on both cranidium and pygidium. The proposed name has been used by Prof. Per Thorslund *in museo*.

Holotype. – An almost complete pygidium, SGU type 3909, Fig. 15H.

Paratype. – An almost complete and well-preserved topotype cranidium, SGU type 3910.

Additional material. – A single incomplete thoracic tergite from the same block as the paratype cranidium, SGU type 5451.

Type stratum and type locality. – Andersö ('Ogygiocaris') Shale, Zone of *Nemagraptus gracilis*. East of Käringnäset, northern coast of Andersön, Sunne Sokn (community), Jämtland, Sweden.

Diagnosis. – Median area of glabella finely striated, with a short but strong sagittal furrow between S3. Pygidium longer than wide, widest posteriorly, with very small first pair of marginal spines opposite end of axis, far in front of large postero-laterally situated second pair; third pair developed as rounded prolongations.

Description. – Cranidium trilobate, almost nine-tenths as long as wide. Median area of glabella five-ninths as long as wide, very slightly convex transversely, with a short but distinct sagittal furrow located between the adaxial tips of S3, and with a prosopon of parallel, fine and dense striae which abaxially are directed subexsagittally, more adaxially in inwardly gentle curves, and between S1 and the occipital furrow in fairly strong curves of various direction (cf. Fig. 15A, G). S1 slightly sigmoidal, strongly impressed, rather broad (exsag.), and the corde between tips of each furrow being about one-quarter the width of median area. S2 convex forwards, sharply defined, narrow (exsag.), the corde between tips being two-sevenths the width of the median area. S3 slightly convex forwards, strongly oblique, quite sharply defined, narrow (exsag.), and with corde between tips being one-eighth the width of the median area. Glabellar tongue bulbous, slightly more than half as long as wide, almost two-thirds as wide as and five-eighths as long as the median area, overhanging the anterior border, and with striae similar to those on the median area arranged in an elliptical

pattern. Preglabellar furrow shallow. Anterior border narrow (sag., exsag.) and list-like, and slightly broader laterally than sagittally. Axial furrow narrow (tr.) and shallow. Palpebral furrow deep, posteriorly with an almost right-angled bend. Anterior rim very slightly convex (tr.), very narrow and passing gradually into anterior border. Palpebral lobe sub-semicircular, at transverse mid-line one-fifteenth as wide as median area, laterally and posteriorly of even width, anteriorly rapidly decreasing and passing gradually into anterior rim, sloping slightly downwards towards palpebral furrow, with a very faint epipalpebral furrow located very slightly closer to the ocular suture than to the palpebral furrow, and with striae subparallel to lateral margin. Occipital furrow very slightly more than half as wide as median area of glabella, convex forwards mesially, concave so laterally, narrow sagittally but rather broad exsagittally. Occipital ring widest (tr.) anteriorly, broadest sagittally, with posterior margin straight, a broad (sag.) but shallow band furrow close to posterior margin producing a sigmoidal cross-section, and with roughly transverse, slightly coarser striae than elsewhere on the cranidium. Occipital node very small and located close to occipital furrow. Posterior fixigenae not preserved in the present cranidium. Thoracic tergite (if conspecific) with an axial ring occupying more than two-thirds the total width, with a conspicuous band furrow, and with prosopon similar to that on the occipital ring; pleurae subquadratic, transversely slightly concave, with a sharp but not particularly pointed postero-lateral corner, and with thin, subexsagittal striae. Pygidium subrectangular, about four-fifths as wide as long, distinctly wider posteriorly than anteriorly, and with width across anterior margin almost twice that of axis. Pygidial axis very prominent, extending almost three-quarters of the sagittal length, strongly convex transversely, gradually tapering rearwards and passing posteriorly imperceptibly into a very shallow but broad postaxial ridge. Articulating half ring very sharply defined posteriorly by the narrow but strong articulating ring furrow. First axial ring well defined, subsequent axial rings gradually effaced rearwards, but at least seven rings are recognized. Pleural fields in general flat, with three pairs of very distinct but shallow, strongly backwardly directed pleural furrows of successively increasing width rearwards, producing a wavy appearance. Striae coarser and less closely spaced than on the cranidium, with a pattern of well-arranged sinuous striae that are concave forwards on the ridges. First pair of marginal spines very small, acute, situated opposite posterior end of axis; second pair large and broad-based but acute, situated at postero-lateral corners of the pygidium; third pair developed only as rounded prolongations of the posterior margin close to the sagittal line.

Dimensions. – The paratype cranidium is 8.8 mm long, and 9.9 mm wide, with the glabellar tongue 3.0 mm long and 5.6 mm wide; the median area of the glabella is 8.8 mm wide. The holotype pygidium is 6.5 mm long sagitally, 7.4 mm long distally, 4.6 mm wide anteriorly and 6.2 mm wide posteriorly (estimated by doubling the width of right half), with the axis 2.6 mm wide anteriorly and approximately 4.8 mm long.

Affinities. – *R. striatella* sp. nov. is closely related to the older *R. schlotheimi* (Billings, 1865, p. 294, figs. 284a–b) from the Middle Table Head Formation and its equivalents in western Newfoundland; strata of approximately middle to upper Llanvirn age, which, in all probability, is its direct ancestor. Their respective cranidia differ only in that *R. striatella* has a short but much more distinct sagittal groove between S3 and that the pattern of the prosopon is slightly different. The lateral glabellar furrows also seem stronger in the Swedish species, but all differences are probably of less importance than the similarities, which support the close relationship. The cranidium of *R. striatella* is also very like that of *R. major* Raymond (1920b, pp. 281–282; see Whittington 1959b, pp. 428–431, Pl. 18, figs. 1–22, 25) from early Caradoc and possibly very late Llandeilo strata in eastern North America, but differs in that the lateral glabellar furrows are stronger. Both have very short (tr.) thoracic pleurae (cf. Cooper 1953, Pl. 8, fig. 11). The pygidia of *R. schlotheimi* (cf. Whittington 1965, Pl. 41, figs. 2, 9–10) and *R. striatella* have an overall similarity, but can be distinguished in several respects. The first pair of very small marginal spines is located opposite the axial end in *R. striatella*, but somewhat further rearwards in *R. schlotheimi*, whereas in the latter the second pair is considerably stouter and longer. Also, the axis is slightly longer in *R. striatella* than in *R. schlotheimi*, causing a relatively shorter distance between the axial and sagittal ends. The pygidium of *R. striatella* differs from that of *R. major* in widening backwards and in having a longer second pair of marginal spines. The three species in question form a closely knit group further discussed below (pp. 52–54).

The cranidium of *R. striatella* is indistinguishable from that of *R. sparsa* Nikolaisen (1983, pp. 292–294, Pl. 15, figs. 2–7) from the Elnes Formation (Zone of *Hustedograptus teretiusculus*), southern Norway. However, the pygidium of the latter differs in being much wider and in having the first pair of marginal spines situated well behind the axial end producing an almost quadratic outline.

Occurrence. – As for type specimens.

Genus *Pugilator* gen. nov.

Name. – From Latin *pugilator*, boxer, fighter who uses the cestus, alluding to the likeness of the cranidium to the palm side of a boxing glove. Gender masculine.

Type species. – *Robergia yukonensis* Churkin, 1966 from the Road River Formation, northern Yukon territory, Canada.

Diagnosis. – A robergioid genus with: narrow (tr.) palpebral lobes, length (exsag.) less than one-third that of cranidium (sag.), extending from behind the abaxial ends of S3 to opposite or slightly behind abaxial ends of S1; glabella moderately expanding between palpebral lobes; glabellar tongue wider than occipital ring and larger than median area of glabella; pygidium with three pairs of well-developed marginal spines.

Included species. – *Robergia deckeri* (Cooper, 1953; *Robergia* sp. Chugaeva 1964; and ?*Remopleurides obtusus* Salter, 1853.

Remarks. – *Pugilator* gen. nov. comprises forms that differ markedly in both the cranidium and the pygidium from those of *Robergia* s.s.

The two North American species included in the genus have been described using complete and well-preserved specimens. *P. yukonensis* has been selected as type species because the holotype is a mature holaspid, that of *P. deckeri* being immature. The epipalpebral furrow has not been reported in any of the species assigned to the new genus. Nevertheless, it seems to be present on the right palpebral lobe of the paratype of *P. deckeri* figured by Churkin (1966, Pl. 4B).

The holotype of *Remopleurides obtusus* Salter (1853, p. 9), a cranidium with four attached thoracic tergites, is from the Killey Bridge Formation (lower Cautleyan) at Desertcreat, Pomeroy, County Tyrone, Northern Ireland. Reed (1952, pp. 109–110) transferred it to *Robergia*, but, like Salter, did not illustrate it. Mr Ronald P. Tripp and Dr J. Keith Ingham are presently revising the Upper Ordovician Pomeroy trilobite fauna and the former has kindly provided illustrations of Salter's type specimen and of additional material. These resemble *Pugilator* in having a fairly small median area of glabella and a large glabellar tongue, but differ from it and *Robergia* in having effaced lateral glabellar furrows and stronger, falcate palpebral lobes extending backwards to opposite the occipital furrow (remopleuridioid condition). ?*P. obtusa* may belong to a separate genus, related to *Pugilator*, although the cranidium is similar to that of *Remopleurides exallos* Webby (1973, pp. 456–457, Pl. 51, figs. 3–12) from the Caradoc Malongulli Formation (Zone of *Dicranograptus hians*) in New South Wales. Therefore the assignment of *obtusa* to *Pugilator* is questionable.

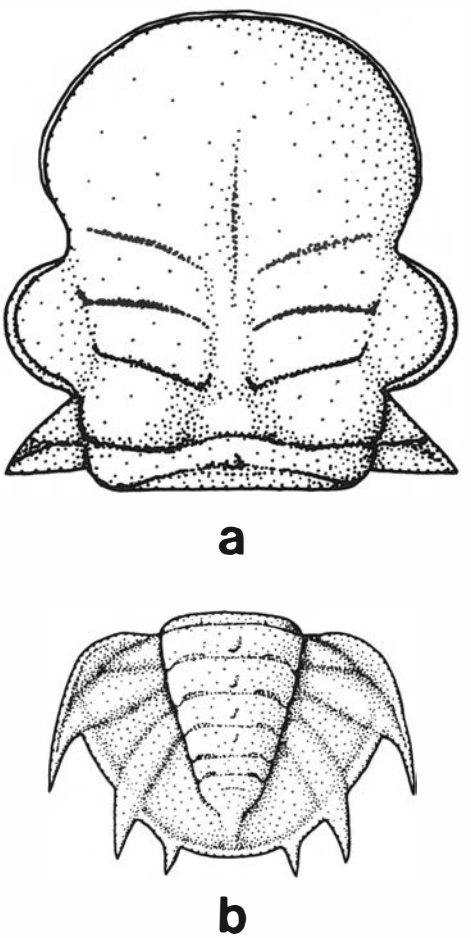

Fig. 8. a–b. Restorations of cranidium and pygidium of *Pugilator yukonensis* (Churkin, 1966), based on Churkin 1966, Pl. 4A and Pl. 5, figs. 4–5.

Pugilator yukonensis (Churkin, 1966)

Fig. 8a–b

1966 *Robergia yukonensis* sp. nov. – Churkin, pp. 41–44, Pl. 4, Pl. 5, figs. 1–5 (descr. and figs. of dorsal exoskeletons and cranidia).

Holotype. – An almost complete dorsal exoskeleton, GSC 19864, 10 m below the top of the Road River Formation about 3 km west of the junction of Iron Creek with the Snake River, northern Yukon Territory, Canada, figured by Churkin 1966, Pl. 4A.

Remarks. – Lenz & Churkin (1966) stated the type horizon to be upper Ashgill in age, based on graptolithes, but this was doubted by Ross & Shaw (1972, p. 16), 'simply because the association of *Robergia*, *Cryptolithoides*, and *Ampyxina* is of Trenton age everywhere else that it has been found'. Their view is supported by Ludvigsen (1975, pp. 680–690, Barnes et al. 1981, correlation chart) and that *P. yukonensis* is of Edenian age, i.e. uppermost Middle/lower Upper Ordovician.

Occurrence. – As for type specimen.

Pugilator deckeri (Cooper, 1953)

Fig. 9a–b

1933 *Robergia athenia* Ulrich [sic] – Decker, pp. 1415, 1419, 1422, 1424–1425, 1434 (recorded and remarks).

1953 *Robergia deckeri* n. sp. – Cooper, pp. 23–24, Pl. 2, figs. 1–6, Pl. 19, figs. 1–2 (descr. and figs. of dorsal

exoskeletons, dorsal exoskeletons with shedded librigenae, cranidium, thoracopygon, thorax and pygidium).

1972 *Robergia deckeri* B. N. Cooper – Ross & Shaw, p. 16, Pl. 1, figs. 16–21 (descr. and figs. of cranidia and pygidia).

Holotype. – An almost complete dorsal exoskeleton with shedded librigenae, USNM 116432a, from zone 4 of the Viola Limestone, Viola Formation, northeast edge of Bromide, Oklahoma, figured by Cooper 1953, Pl. 2, fig. 5.

Remarks. – The cranidium from the Omulevsk Mountains, northeastern U.S.S.R., described and figured as *Robergia* sp. by Chugaeva (1964, p. 29, text-fig. 5, Pl. 1, fig. 12) is remarkably similar to those of *P. deckeri*, and may be conspecific. However, the Siberian cranidium seems to have the S3 slightly more adaxially and posteriorly situated. The stratigraphical horizon is given as Middle Ordovician (Darpirskij horizon), but Chugaeva (1964, p. 18, Tables 1, 8) lists it from the Syachanskij and Volchinskij Formations and the Kharkindzhinskij horizon, with ages spanning from middle to uppermost Caradoc.

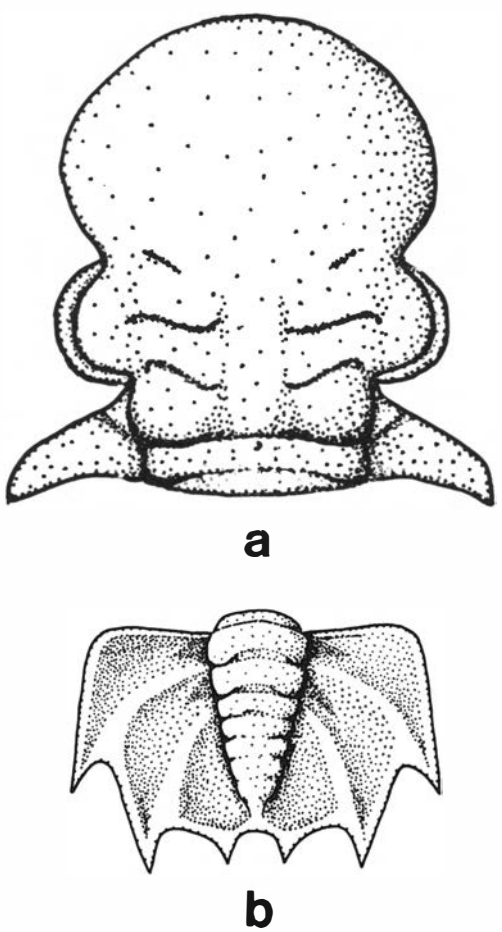

Fig. 9. a–b. Restorations of cranidium and pygidium of *Pugilator deckeri* (Cooper, 1953), based on Cooper 1953, Pl. 2, fig. 4, Pl. 19, fig. 1.

Occurrence. – Viola Formation: northeast edge of Bromide, on U.S. Highway 77, and 3.2 km west of Nebo Store south of Sulphur, all Oklahoma, Copenhagen Formation (upper 17 m): east side of Antelope Valley, and Hill 8308 (see Ross & Shaw 1972), both Nevada. Caesar Canyon Limestone: northern Toquima Range, Nevada.

Genus *Arator* gen. nov.

Name. – From Latin *arator*, ploughman, farmer, alluding to the plough-like appearance of the cranidial anterior border. Gender masculine.

Type species. – *Robergia marianna* Koroleva, 1965 from the upper Llandeilo/lower Caradoc Tselinograd horizon, Lidievka, Stepnyak, Belyi Kordon, northern Kazakhstan, U.S.S.R.

Diagnosis. – A remopleuridioid genus with: length of palpebral lobes more than half that of cranidium (sag.), extending backwards to opposite occipital furrow and without epipalpebral furrows; glabellar tongue narrower (tr.) than occipital ring, much smaller than median area of glabella; anterior border falcate, strong and wider (tr.) than glabellar tongue, thoracic tergites with very short (tr.) pleural fields; pygidium rectangular, wider than long, and with three pairs of small, acute marginal spines situated transversally at posterior margin.

Included species. – *Robergia marianna* Koroleva, 1965, *asiatica* Koroleva, 1982, probably also (?)*Apatokephalus* sp. Chang & Fan 1960 and *Robergia barrandei* sensu Balashova 1959, and ?*Robergia intecta* Koroleva, 1982.

Remarks. – Figured material of *A. marianna* and *A. m. asiatica* (see Koroleva 1965, Pl. 2, figs. 9–12; 1982, Pl. 16, figs. 7–10, Pl. 17, figs. 1–6) and studied replicas of type and additional material of both show how closely related they are. In fact the cranidium figured by Koroleva (1982, Pl. 16, fig. 8; herein Fig. 16B) is intermediate between the two subspecies. Koroleva's nominate form has been selected type species because it is the better known, even though material of *asiatica* has the characteristic anterior cranidial border better displayed.

The two cranidia from the Tollevskaja Formation, 13 km above the outlet of Bolshoj Osevoj, eastern Taimyr, described and figured as *Robergia barrandei* by Balashova (1959, pp. 25–26, Pl. 1, figs. 18–19; also 1960, pp. 25–26, Pl. 1, figs. 18–19) may belong here. Both are incomplete, but show the characteristic broad (tr.) palpebral lobes, a large median glabellar area with strong lateral glabellar furrows and a narrow (tr.) glabellar tongue.

The external mould of the incomplete cranidium from Llanvirn(?) strata of Ch'i-lien Mountains, China, described and figured by Chang & Fan (1960, p. 113, Pl. 3, fig. 18) is so like *A. asiaticus* to suggest that they might be synonymous.

Information from M. Apollonov (pers. comm., Sept. 1985) suggests that *Arator* n. gen. is represented by species in the Bestamak Formation (Tselinograd horizon, zone of *Nemagraptus gracilis*) and in the Anderken horizon (Zone of *Dicranograptus clingani*) of the Chingiz Range, Kazakhstan. Apollonov (1975, pp. 377–378) believed these to belong to 'a new genus related to *Robergia*'.

Arator mariannus mariannus (Koroleva, 1965)

Figs. 10a–d, 16A–C

1965 *Robergia marianna* sp. nov. – Koroleva, pp. 158–159, Pl. 2, figs. 9–10, 12, *non* fig. 11 [= *A. m. asiaticus*] (descr. and figs. of cranidia and pygidium).

1968 *Robergia marianna* Kor. – Apollonov, p. 82 (listed).

1968 *Robergia marianna* – Apollonov *in* Nikitin et al., correlation chart (listed).

1972 *Robergia marianna* Kor. – Apollonov *in* Nikitin, p. 138, Tables 10–11 (listed).

1980 *'Robergia' marianna* Kor. – Apollonov *in* Nazarov & Popov, p. 11 (listed).

1982 *Robergia marianna* Koroleva – Koroleva, pp. 89–91, Pl. 16, figs. 7–10, Pl. 17, figs. 1–2 (descr. and figs. of holotype, cranidium, librigena, thoracic tergites and pygidia).

1985 *Robergia marianna* Kor. – Apollonov *in* Kolobova, p. 168 (quoted Apollonov *in* Nazarov & Popov 1980).

Holotype. – A cranidium, 1101/140 GM IGN, from the upper Llandeilo/lower Caradoc Tselinograd horizon

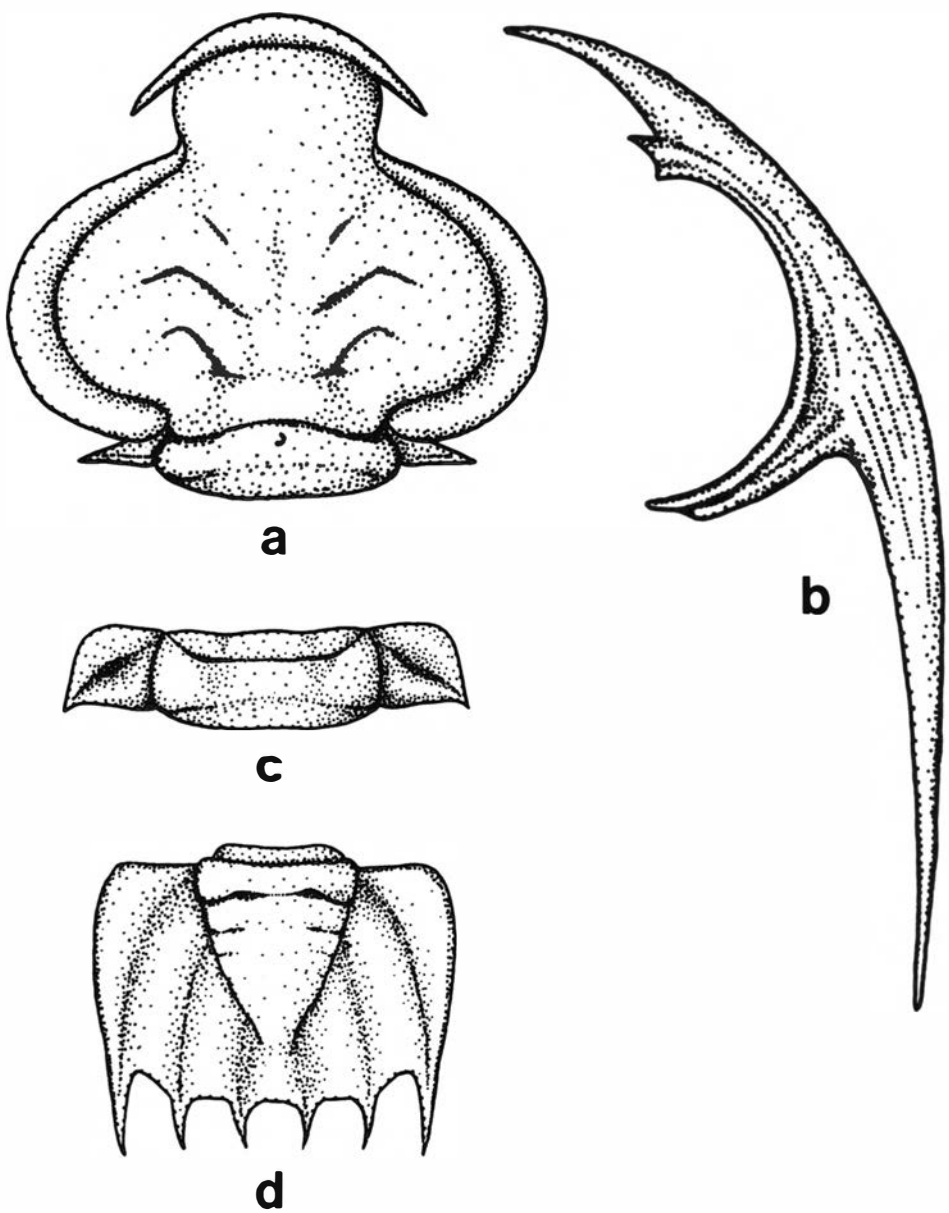

Fig. 10. Restorations of *Arator mariannus mariannus* (Koroleva, 1965). a. Cranidium based on Fig. 16A–B. b. Librigena based on Koroleva 1982, Pl. 17, figs. 2a–b. c. Thoracic tergite based on Koroleva 1982, Pl. 17, fig. 1. d. Pygidium based on Fig. 16C.

about 12 km east of the settlement Lidievka, Stepnyak district, Belyi Kordon area, northern Kazakhstan, figured by Koroleva 1965, Pl. 2, fig. 9; also 1982, Pl. 16, fig. 7, see Fig. 16A herein.

Diagnosis (translated from Koroleva 1982). – Cranidium small and flat. Glabella large, expanded between eyes, three pairs of fairly curved transversal furrows, and anteriorly prolonged into a weakly convex and moderately wide tongue.

Description (translated from Koroleva 1982). – Cranidium small, with a straight posterior margin, anteriorly extended into a moderately wide and weakly convex tongue, and with its maximum width across mid-length of palpebral lobes and median pair of lateral glabellar furrows. Glabella large, with a weakly convex anterior part and a flattened posterior half part, and on which are three pairs of distinctly impressed lateral furrows. The anterior pair is almost straight and directed outwards forwards. The median pair is considerably longer than the other pairs and fairly convex forwards. These latter are situated almost on the transversal line of maximum width, abaxially not reaching the axial furrows and not touching each other. Posterior pair approximately as long as the anterior pair, but is on the contrary curved, and distance between adaxial ends somewhat larger than in the anterior and median pairs. Occipital furrow straight and deep. Occipital ring wide and weakly convex. Eyes wide, finely reticulated, gently convex, separated from glabella by deep convex palpebral furrows and moderately wide palpebral lobes. The eyes are extending from immediately after the occipital furrow and running sausage-shapedly along lateral margins of glabella to the lateral margins of the glabellar tongue. A narrow anterior border is present. Librigenae narrow and sickle-shaped, triangular in outline, somewhat expanded at posterolateral corners, with the lateral part developed as a flat, sausage-shaped and small border, and provided with long spines. Only a specimen consisting of two thoracic tergites is present; axial rings apparently smooth, with short pleurae bearing diagonal furrows which are deepest mesially. Pleural ends gently acute. Pygidium almost rectangular in outline (slightly wider than long). Axis broad anteriorly but rapidly tapering backwards, ending in an acute angle, and not reaching the posterior margin of the pygidium. Articulating half ring narrow, and, in addition, there is a distinctly and prominent first axial ring, whereas the following two rings are only weakly indicated laterally. Pleural areas of pygidium flattened, and on which are visible three pairs of very weak, vaguely wavy-shaped furrows which posteriorly end in small spines. Thin terrace lines are visible on large parts of the pygidial surface.

Remarks. – Replicas of both the holotype and paratype cranidia figured by Koroleva (1965, Pl. 2, figs. 9–10; also 1982, Pl. 16, figs. 7–8) are illustrated herein (Fig. 16A–B). These show some dorsal exoskeleton and it is clear that the epipalpebral furrow is lacking. There also seems to be a total absence of a prosopon on the median area of the glabella and the occipital ring. The thoracic tergites (Koroleva 1982, Pl. 17, fig. 1; herein Fig. 10c) have much shorter pleurae (tr.) than those of both *Robergia* and *Pugilator*. Moreover, the pleural furrows are rather deep and give the pleurae a distinct relief as opposed to the flat pleurae in *Robergia*. As in *Robergia*, fulcral processes and sockets are lacking.

Occurrence. – Tselinograd (Zone of *Nemagraptus gracilis*) and Erkebidaik (Zone of *Diplograptus multidens*) horizons in the Stepnyak and Ishim River Regions, the Bestamak Formation in the Tselinograd horizon in the Chingiz Range, and Dulankara horizon (?Zone of *Pleurograptus linearis* [probably Zone of *Nemagraptus clingani*, Apollonov pers. comm., Sept. 1985]) in the Chu-Ili Mountains, all Kazakhstan, U.S.S.R.

Arator mariannus asiaticus (Koroleva, 1982)

Figs. 11a–b, 16D–E

1965 *Robergia marianna* sp. nov. [partim] – Koroleva, pp. 158–159, Pl. 2, fig. 11 only (descr. and fig. of cranidium).

1982 *Robergia marianna asiatica* Koroleva, subsp. nov. – Koroleva, pp. 91–92, Pl. 17, figs. 3–6 (descr. and figs. of cranidia and pygidium).

Holotype. – A small cranidium, 1101/126 GM IGN, from the upper Llandeilo/lower Caradoc Tselinograd horizon, east of Lidievka, Stepnyak district, Belyi Kordon, northern Kazakhstan, figured by Koroleva 1982, Pl. 17, figs. 4a–b.

Diagnosis (translated from Koroleva 1982). – Cranidium small and flat. Glabella strongly expanded between palpebral furrows, with anterior part expanded into a convex narrow tongue. On the wide, flattened part of the glabella there are three pairs of gently curved, roughly transversal furrows. Occipital ring wide. Librigenae narrow, ending in long but fine spines.

Description (translated from Koroleva 1982). – Cranidium small with a large flat glabella that is strongly expanded between palpebral furrows and anteriorly extended into a moderately wide, weakly convex tongue. There are three pairs of lateral furrows on the flattened posterior half part of the glabella. Anterior pair short, situated closely behind base of glabellar tongue, and directed outwards and slightly forwards. Median pair considerably longer than first pair, weakly convex and running roughly in a transverse direction. Posterior pair slightly longer than anterior pair but shorter than median pair, adaxial ends curved towards occipital ring, abaxial ends appear transversely directed. Occipital furrow

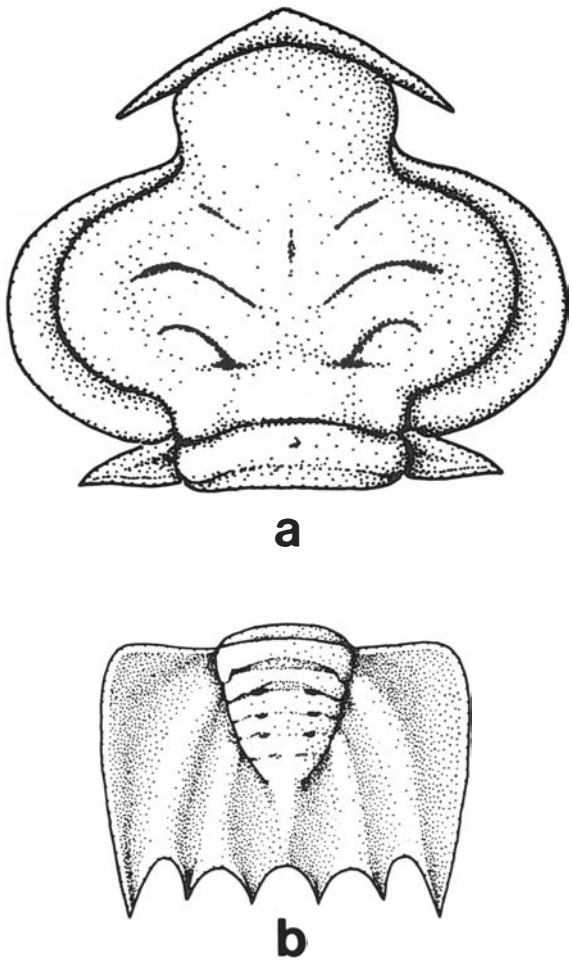

Fig. 11. Restorations of *Arator mariannus* (Koroleva, 1965) *asiaticus* (Koroleva, 1982). a. Cranidium based on Fig. 16D–E. b. Pygidium based on Koroleva 1982, Pl. 17, figs. 6a–b.

narrow. Occipital ring wide. Palpebral furrows deep and comparatively wide. Palpebral lobes gently sloping towards glabella. Eyes wide, gently curved, and consisting of numerous facets. Fixigenae apparently reduced. Librigenae gently flattened at postero-lateral part, very narrow laterally, and ending in long but narrow spines. Pygidium almost rectangular (slightly wider than long). Axis coniform, wide and convex, and with posterior end not reaching the posterior margin. A distinct articulating half ring is present on the anterior of the axis, whereas the second axial ring is incised but almost invisibly as small pits on both sides of the axis. Pleural field surrounding axis flat, and on which three pairs of low grooves are faintly visible laterally. Posterior margin of pygidium ending in three pairs of quite small but acute spines. The posterior half part of the pygidium is covered with thin terrace lines.

Remarks. – The small cranidium illustrated herein (Fig. 16D–E) was not figured by Koroleva (1982), but it is to be regarded as a paratype (M. N. Koroleva, pers. comm., Febr. 1986). It is an internal mould lacking epipalpebral furrows. The glabella is slightly wider than those figured by Koroleva (1982, Pl. 17, figs. 3–5), but narrower than in *A. m. mariannus*. Both are closely related, but *A. m. asiaticus* differs from *A. m. mariannus* (cf. Koroleva 1982, p. 92) in having broader palpebral lobes and less oblique lateral glabellar furrows. Furthermore, it has a more prominent, distinctly falcate anterior border and a pygidium that is slightly narrower.

Occurrence. – Tselinograd (Zone of *Nemagraptus gracilis*) and Erkebidaik (Zone of *Diplograptus multidens*) horizons in the Lidievka Formation, east of the small settlement Lidievka, Stepnyak district, Belyi Kordon, northern Kazakhstan, U.S.S.R.

Genus *Eorobergia* Cooper, 1953

Type species. – *Robergia marginalis* Raymond, 1925 by original designation, from the Lenoir Limestone, 1.5 km east of Bluff City, Tennessee, U.S.A.

Remarks. – Several species and informally named forms have been attributed to the genus since the issue of the Treatise on Invertebrate Paleontology, Part *O* (Moore 1959), most of them from various parts of the U.S.S.R. Thus the presently included species exhibit a wide range of morphotypes from forms with a smooth median glabellar area to forms with three pit-like lateral glabellar furrows, forms with a very narrow glabellar tongue to those with a very broad one, and from forms with a row of pits on the anterior border to forms without. An emended generic diagnosis and a list of all species included to date is given by Chugaeva (1973, pp. 51–52). To this may be added *E. assai* (Weber, 1932, p. 8 [111], Pl. 4, figs. 50–51; also 1948, p. 12, Pl. 2, figs. 1–2, 3–4?). The species group centred around the type species (*E. marginalis*) includes *E. grandis* Whittington (1965, pp. 380–383, Pl. 43, Pl. 44, figs. 1–2), *E. summa* Burskij (1966, pp. 39–41, Pl. 2, figs. 1–4), *E. lata* Chugaeva (1973, pp. 53–55, Pl. 3, figs. 2–5) and similar Lower Ordovician forms that have been assigned to *Apatokephalus* (e.g. *A.* sp. I Chugaeva 1973, pp. 50–51, Pl. 2, figs. 5–7 from El'genchaksk Mountains in northeastern U.S.S.R.). It seems likely that the *E. marginalis* species group has developed from *Apatokephalus* or from a closely related form. This is illustrated by the recently described *Apatokephalus hunjiangensis* Duan & An (1986, pp. 75–76, Pl. 20, figs. 1–5, 7–9) from the upper Tremadoc Yehli Formation (Koraipsis Zone), Hunjiang, southern Jilin, northeastern China. The cranidium of *A. hunjiangensis* is remarkably similar to that of *E. breviceps*, and the pygidium has long and broad pleural spines like those of *E. marginalis* and its allies. Several undescribed remopleuridid genera occur in the Ordovician deposits of Kazakhstan including one which is similar to the more aberrant species presently included in *Eorobergia* (M. K. Apollonov, pers. comm., Oct. 1985).

***Eorobergia breviceps* (Raymond, 1925)**

Fig. 16F–K

1925 *Robergia breviceps*, sp. nov. – Raymond, pp. 62–63 (descr.).

Holotype. – A small but almost complete cranidium, MCZ 1727, from lot 22, concession IV, boulder no. 2, Normanskill Conglomerate, 3.3 km north of Mystic, Missiquoi County, Quebec, Canada, selected and described by Raymond 1925, pp. 62–63, and figured herein Fig. 16F–G. Two additional cranidia from the same boulder were mentioned by Raymond and these, both numbered MCZ 3276, are probably those (R. C. Eng, pers. comm., Sept. 1985) from the same locality. These are illustrated herein (Fig. 16I–J) as paratypes.

Diagnosis. – An *Eorobergia* species with evenly rounded palpebral lobes not reaching as far back as opposite occipital furrow, two pairs of lateral glabellar furrows, short (sag.) glabellar tongue, and a very large occipital ring.

Additional material. – Two incomplete thoracic tergites (Fig. 16H, K), one associated with the holotype and the other with the paratype cranidium.

Description. – Cranidium urceolate, slightly wider than long in the smaller holotype but estimated to be nearly as long as wide in the larger paratypes. Median area of the glabella very nearly as wide as its length, only slightly wider than occipital ring, and with mesial part gently convex (tr.). Glabellar tongue bulbous, sloping steeply downwards forwards, and with gently convex anterior and lateral margins. Occipital ring very prominent, with posterior margin straight and even, and with a small but distinct occipital node located a short distance from the anterior margin. Occipital furrow narrow but deep. Only two pairs of lateral glabellar furrows present; S1 very strong, short, slightly bifurcate with the anterior branch strongly convex; S2 much weaker, straight, and directed obliquely backwards inwards from the junction with the anterior end of the palpebral furrow. Anterior border well defined by deep anterior border furrow, strongly convex (sag., exsag.), with fine, transverse striae and without a row of pits along the posterior margin. Anterior branches of facial suture diverging. Palpebral lobes sausage-shaped and evenly rounded, well set off from median area of glabella by deep palpebral furrows, strongly convex (tr.), and with faint traces of an epipalpebral furrow postero-laterally. Posterior area of fixigenae wedge-shaped. The whole glabellar surface with a prosopon of tiny wrinkles arranged in a Bertillon pattern. Thoracic tergite transversely rather convex. Axial ring occupying almost half the width of the tergite, strongly convex transversely, with a very broad (sag., exsag.) and deep articulating furrow, and with a prosopon of somewhat disarranged, fine lines. Axial furrow deep but well defined only posteriorly. Pleura slightly narrowing outwards, deflected but elevated a short distance from the axial furrow to form very low fulcral processes and sockets. Anterior and posterior pleural bands separated by a conspicuous ridge running slightly obliquely backwards and much closer to the anterior than to the posterior margin of the pleura. Prosopon made of fine, almost exsagittal, wavy lines.

Remarks. – *E. breviceps* differs from members of the *E. marginalis* species group in having more rounded palpebral lobes, a more dominant occipital ring, only two pairs of lateral glabellar furrows of which S1 is more anterior, a more anteriorly situated occipital node, and in lacking the row of pits along the posterior margin of the anterior border and the lateral flexures (cf. Whittington 1965, p. 381) on the occipital ring. Nevertheless, *E. breviceps* still falls within the generic diagnosis.

The fragmentary and poorly preserved cranidium figured as apatokephalid gen. et sp. indet. A by Rozova (*in* Rozova et al. 1965, p. 126, Pl. 12, fig. 19) from the lower third of the Tremadoc Maslyaninsk horizon in the Chypinskaj Formation in northwestern Salair, Novosibirsk, U.S.S.R. is like *E. breviceps* and differs only in having a shorter (tr.) occipital ring. This may indicate that *E. breviceps* branched off from the morphotype of the type species complex as early as in Tremadoc times.

E. breviceps also differs from *E. insignis* Petrunina (*in* Petrunina & Severgina 1962, pp. 84–85, Pl. 1, figs. 4–8) from the Bugryshikhinsk Formation (Caradoc?) in Bugryshikh, Altay Mountains, in having a shorter cranidium, more anteriorly located S1 and a broader (sag., exsag.) occipital ring.

Occurrence. – As for type specimens.

Remarks on the phylogeny of *Robergia*

One group of species here assigned to *Robergia* form a closely knit unit that may easily be recognized by their pygidium. They include in stratigraphical appearance *R. schlotheimi* (Billings, 1865), *R. striatella* sp. nov. and *R. major* Raymond, 1920. *R. athenia* Butts, 1926 also belongs here, but according to Whittington (1959b, p. 428) is most probably a subjective synonym of *R. major*. The species of this unit are characterized by having a fairly narrow pygidium with a very small first pair of marginal spines that are located more or less opposite the posterior end of the axis. *R. schlotheimi* occurs in eastern North American strata corresponding approximately to middle to upper Llanvirn in European terms (Barnes et al. 1981) and is therefore presumably the oldest of all known *Robergia* species. It should be noted here that the librigena and pygidium from the Llanvirn *confinis* Flags of Girvan described and figured by Tripp (1962, pp. 5–6, Pl. 1, figs. 18a–b, 19) as *Robergia* sp. probably do not belong in the genus. The librigena is certainly from a remopleuridid, but not necessarily *Rob-*

ergia, whereas the poorly preserved pygidium most probably belongs to a cybeline. The librigena from the Auchensoul Limestone (?upper Llanvirn) at Auchensoul Bridge, Girvan, figured by Tripp (1979, Pl. 37, fig. 11) as *Robergia* sp. cannot univocally be assigned to this genus, but may as well belong to *Robergiella*, which occurs commonly in the somewhat younger Balclatchie Group in the same district (Tripp 1980, Table 1). *Robergia striata* Endo (1932, pp. 109–110, Pl. 38, fig. 3) from the Llanvirn Siliangssu Formation near Huangbayi,

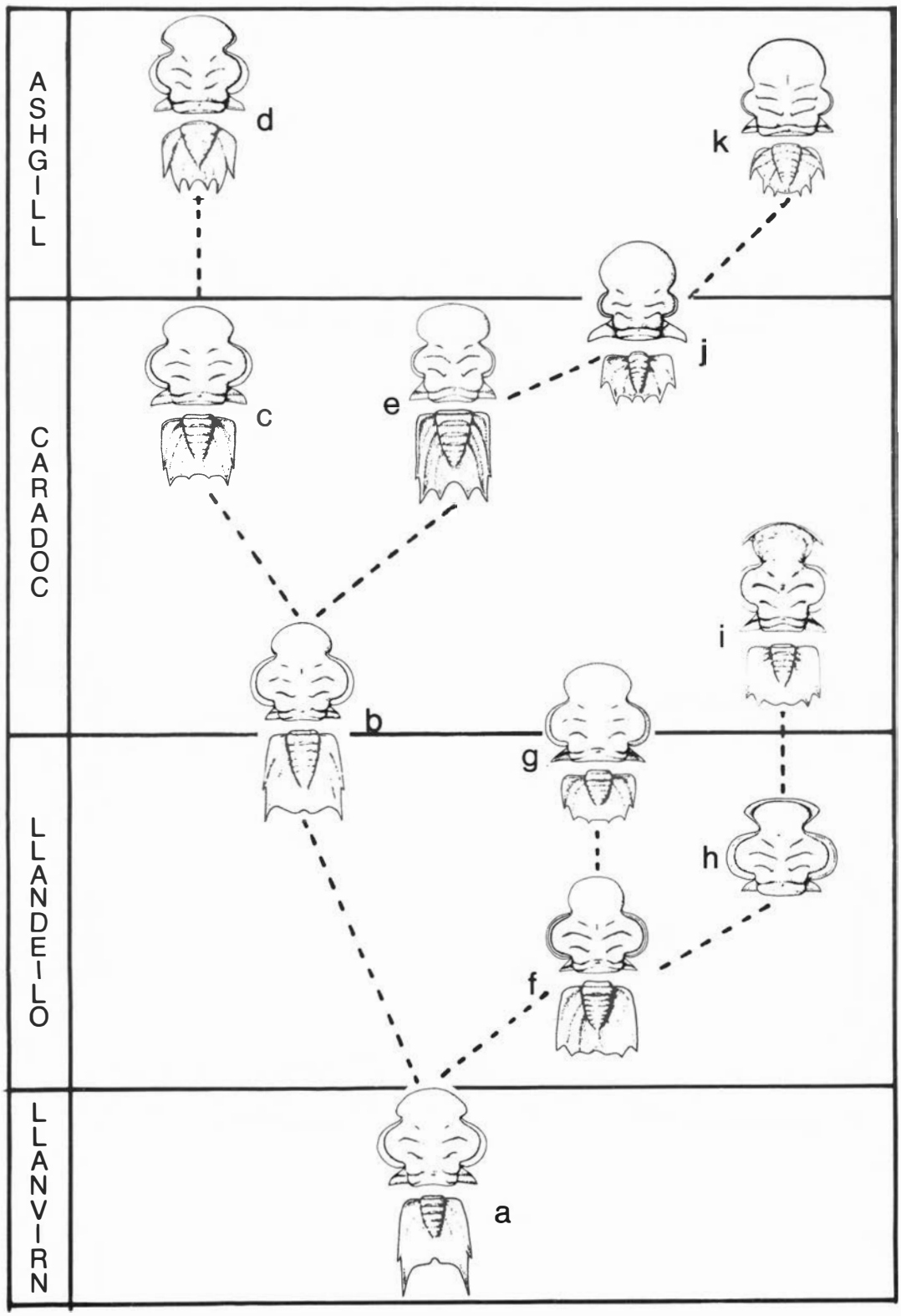

Fig. 12. Proposed relationship between *Robergia* (a–i) and *Pugilator* gen. nov. (j–k), based on the following species: a. *Robergia schlotheimi*; b. *R. striatella*; c. *R. major*; d. *R. sinensis*; e. *R.* sp. nov.?; f. *R. sparsa*; g. *R. microphthalma*; h. *R. scanica*; i. *R. barrandii*; j. *Pugilator deckeri*; k. *P. yukonensis*. Stratigraphical occurrence approximate, series lengths not to scale.

southern Shaanxi, China, has previously been transferred to *Remopleurides* by several authors, i.e. Reed (1935, p. 11), Whittington (1959b, p. 437), Lu (*in* Lu et al. 1965, p. 549; 1975, pp. 110, 300–301), Chou & Cheng (1975, p. 151, Pl. 19, fig. 3) and Chang & Jell (1983, p. 206). It has a prominent preglabellar field and was thought to belong to *Robergiella* by Nikolaisen (1983, p. 277). However, judging from Chang & Jell's illustrations (1983, Fig. 6E–F) it is probably best included in *Sculptaspis* Nikolaisen, 1983. *R. striatella* is most probably a direct derivative of *R. schlotheimi* although not appearing before late Llandeilo/early Caradoc. Its cranidium is, as pointed out above (p. 46), remarkably similar to that of *R. schlotheimi* and only minor changes have taken place in the pygidium. The long and dominant second pair of pygidial marginal spines in *R. schlotheimi* have become considerably shortened, whereas other characters have largely been retained. Continuing that trend leads to the pygidium of the third member of this evolutionary stock, *R. major*. It appears in widely spread deposits of middle to late Caradoc age in North America, and has, in addition to the further reduced second pair of pygidial marginal spines, simultaneously developed a wider pygidium. The form included in *R. major* by Ross & Shaw (1972, pp. 16–17, Pl. 1, figs. 8–15) is here regarded as probably a new species. It has a rather large and wide glabellar tongue, rather short palpebral lobes and a quite narrow pygidium with strong pleural ribs and a strong third pair of marginal spines. It seems likely that this latter form branched off from the *R. schlotheimi–R. major* lineage and invaded the central North American platform during its submergence. Both the cranidial and pygidial features of this form, apart from the pygidium being quite narrow, point towards development of characteristics of the new genus *Pugilator*. Ross & Shaw (1972, p. 17) recorded both '*R. major*' and *P. deckeri* from Nevada, and stated that the former presumably occurs stratigraphically lower than the latter as in the Appalachian sections. They recorded, however, a single cranidium of the *P. deckeri* type associated with '*R. major*'. It therefore seems likely that the Nevadian form in late Caradoc time evolved into *Pugilator* by simply increasing the size of the glabellar tongue, shortening the palpebral lobes, widening the pygidium and strengthening the pleural ribs. Tendency to increase the glabellar tongue and develop long and coarse pygidial spines may have terminated in the somewhat 'atypical' pygidium of the Ashgill *P. yukonensis* (Churkin, 1966) from the Northwest Territory of Canada. If the pygidium of the latter is compared to that of the complete but not fully grown specimen of *P. deckeri* on the slab figured by Cooper (1953, Pl. 19, fig. 1) or the pygidia figured by Ross & Shaw (1972, Pl. 1, figs. 18–19), it is not difficult to conceive *P. deckeri* as a forerunner of *P. yukonensis*. Although only the cranidium is known of *Robergia* sp. Chugaeva (1964, p. 29, Pl. 1, fig. 5) from uppermost Middle Ordovician strata of northeastern U.S.S.R., it seems to agree with that of *P. deckeri* and may well be conspecific. On the other hand, the Chinese middle Ashgill *R. sinensis* has a pygidium with marginal spines arranged in a similar pattern as in the eastern North American specimens of *R. major*. This is especially obvious when compared with pygidia assigned to *R. athenia*, here regarded synonymous with *R. major*. Thus in late Caradoc time the *R. major* species complex gave rise to two uppermost Caradoc–Ashgill evolutionary branches; one that terminated in *R. sinensis* and one that terminated in *Pugilator*.

The remaining species of *Robergia* (*sensu stricto*), having isospinose pygidia, form a far more heterogeneous group than that discussed above. They are European species, in respect of today's geographical position. The group comprises in presumed stratigraphical appearance *R. sparsa* Nikolaisen, 1983, *R. scanica* Hadding, 1913, *R. microphthalma* (Linnarsson, 1875) and *R. barrandii* (Etheridge & Nicholson, 1879). *R. sparsa* is seemingly the oldest. It has been found in limestone lenses from the Ogygiocaris Series from just above the underlying Helskjær Shale and Limestone (upper Llanvirn, approximately corresponding to the zone of *Didymograptus murchisoni*) at the road section between Nydal and Furnes Church in the Nes–Hamar district, southern Norway. It is tempting to assume that *R. sparsa* developed from *R. schlotheimi*, the only stratigraphically earlier species known, or that both derived from an unknown ancestor. The cranidia of the two species are remarkably similar, both in shape and in prosopon, whereas their respective pygidia are quite different. Nevertheless, a deviation of *R. sparsa* from *R. schlotheimi* is still conceivable. The necessary steps involve a general widening of the pygidium with a shortening of the second pair of marginal spines whilst the first pair became more prominent. An evolutionary trend in the Llanvirn/Llandeilo times that attempted shorter pygidia may have terminated in the type species, *R. microphthalma*.

The cranidium is unfortunately the only part of *R. scanica* known. It differs from that of other species in having a conspicuous anterior border and a small glabellar tongue. These are characters found only in juvenile specimens of other species. It thus seems likely that *R. scanica* evolved by arrested development or partial neoteny. The general shape of the lateral glabellar furrows and palpebral lobes indicates that it descended from the *R. sparsa–R. microphthalma* lineage. A somewhat aberrant cranidium is present in *R. barrandii*. However, it has a distinct anterior border that may indicate that it developed from *R. scanica* or a similar form. Its pygidium is well known and is in gross morphology quite similar to that of the solely Scandinavian lineage above, which may support the assumption that it originated from that region. A possible link between late Llandeilo–early Caradoc trilobites of Scandinavia and the Girvan area has earlier been observed among proetids by Owens (1970, pp. 315, 320) and among calymenids by Siveter (1976, p. 392), and in more general terms by Whittington & Hughes (1972).

In addition to all the forms discussed above, *Robergia* sp. nov. was listed from the Tselinograd horizon, Bestamak Formation (Zone of *Nemagraptus gracilis*) at the bank of the river Chagan in the Chingiz Range, Kazakhstan by Apollonov (*in* Nazarov & Popov 1980, p. 9); material of which I have not seen.

Unfortunately, hypostomes which might provide a key to phylogeny are poorly known. The hypostome said to be bifurcated with very long prongs that Raymond (1920b, p. 281; 1925, p. 60) assigned to *R. major* was rejected by Whittington (1959b, p. 429). Whittington had studied Raymond's original material but thought other subsequently collected topotype hypostomes to be conspecific. The peculiar hypostome of *R. schlotheimi* (cf. Whittington 1965, Pl. 41, figs. 3–4, 7) has as yet its equal only in the type species. Otherwise, a comparable hypostome is that described and figured by Ross (1953, p. 635, Pl. 62, fig. 14) as questionably belonging to *Menoparia genalunata* Ross, 1951 from the lower Ordovician Garden City Formation of Utah. It may therefore give a hint on the origin of *Robergia*. Moreover, Whittington (1959b, p. 431) was able to point out similarities between immature cranidia of *Robergia* and *Menoparia*. It is possible here to follow an evolutionary trend that involves an enlargement of the maculae. They are relatively small in *Menoparia*, considerably larger and termed oval areas, but still well separated posteriorly in *R. schlotheimi*, and terminating in the very large oval areas that are separated posteriorly only by a very fine furrow in *R. microphthalma*. Apart from *R. schlotheimi* and *R. microphthalma*, the hypostome is known in *R. major* (cf. Whittington 1959b, p. 429, Pl. 18, figs. 8–14) and *R. barrandii* (cf. Tripp 1980: Pl. 1, fig. 27, text-fig. 3h). The hypostomes of *R. major* and *R. barrandii* are more different from those mentioned above than expected for a moderately changing part of the exoskeleton as the hypostome usually is, and Whittington did not assign his hypostomes to *R. major* with absolute certainty. It is a bit puzzling that the hypostomes of the latter two species are quite similar to those of several European species of *Remopleurides*. Moreover, it cannot be excluded that these hypostomes may belong to *Robergiella*. That genus occurs together with *Robergia* both in the lower part of the Edinburgh Limestone in Virginia and in the lower Balclatchie group at Girvan.

A minute remopleuridid cranidium from the presumed Middle Ordovician beds at Na Yan, Pho Binh Gia, east Tonkin, Vietnam, described and figured by Patte (1926, p. 44, Pl. 2, fig. 3) as *Remopleurides* sp., was suggested probably best transferred to *Robergia* by Kobayashi (1960a, p. 40) and again later but then more in doubt by Kobayashi & Hamada (1978, pp. 14–15). Judging from Patte's illustration, the cranidium differs markedly from equal-sized cranidia of *Robergia* and is safely not included here. It may better be compared with immature cranidia of *Robergiella* s.l. *nasuta* Lu (1957; see Lu 1975, Pl. 3, figs. 17–18).

Koroleva (1982, pp. 92–95, Pl. 18, figs. 1–2) also erected two new species, each founded on a single remopleuridioid cranidium; *Robergia minima* from upper Llandeilo and *R. intecta* from upper Caradoc strata, the latter from northeast of the settlement Akbastau, southwest Chingiz, Kazakhstan. *R. intecta* is a very poorly preserved internal mould. It has proportions similar to those of *A. m. mariannus*, but seems to have a smooth median area and rather narrow (tr.) palpebral lobes, and may probably best but very doubtfully be included in *Arator*. *R. minima* has a very narrow (tr.) glabellar tongue and short, deep and rather oblique lateral glabellar furrows. It may thus be compared with Middle Ordovician forms from northeastern U.S.S.R. assigned to *Eorobergia*, e.g. *E. plana* Chugaeva (1964, pp. 35–37, Fig. 9, Pl. 2, fig. 5) and *E. tscherskyi* Chugaeva (1964, pp. 37–38, Fig. 10, Pl. 2, fig. 6), and to similar undescribed Middle Ordovician forms from Kazakhstan (Apollonov photograph and pen drawings in pers. comm., Sept. 1985). The remopleuridids had their origin and evolutionary centre in central Asia as is obvious from the great variety of both described and undescribed genera from that part of the continent, and particularly from Kazakhstan. Thus a more thorough and reliable cladistic model for the genera discussed in this section must await description of at least the Kazakhstanian forms.

Distribution of *Robergia*

Robergia occurs in deep water dark shales and limestones of the slope facies on both sides of the present north Atlantic region. As emphasized by Shaw & Fortey (1977, p. 434), robergioids are commoner in the upper than in the deeper slope facies deposits. Menzies et al. (1973, pp. 243–253) have shown in a study of recent isopods that deep-water conditions act as a barrier to the fauna, and particularly so at low latitudes. But, however, they noted that maximum geographical distribution of the fauna is in the 'archibental zone of transition' (ibid., p. 317), a zone that has the thermocline as upper limit and which varies greatly in depth dependent on the latitude. This zone may be correlated to the 'slope' facies and intervening abyssal conditions may thus explain the division of 'American' and 'European' *Robergia* stocks. In the Llanvirn and most of the Llandeilo the Iapetus ocean seems to have formed a barrier to *Robergia* as well as other trilobites. Nevertheless, the 'American' *R. striatella* in the lower allochthonous deposits of Jämtland, Sweden, indicates that a connection must have existed between the faunas flanking the Iapetus Ocean. A Laurentian influence of trilobites in the lower allochthonous Llanvirn–Llandeilo deposits of the northern Oslo Region (adjacent to that of Jämtland) has been notified repeatedly (e.g. Nikolaisen 1962 [written communication in *Fossilnytt*, Paleontological Museum, Oslo, p. 14]; 1983, pp. 287–288; Whittington 1965, pp. 424, 427; Wandås 1984, pp. 236–237). Moreover, it is not impossible that the Llanvirn–lower Caradoc dark shales/limestones of

North America and the Balto-Scandian lower allochthon were deposits of the same ocean floor as shown between parts of western North America and China in the late Cambrian (Cook & Taylor 1975; Eldredge 1977, pp. 314–315). More likely the slope facies of North America and the lower allochthon of Balto-Scandia lay in the psychrosphere between the North American and the Acado-Baltic Faunal Provinces in the Late Cambrian as shown by Taylor & Forester (1979, pp. 410–411, Fig. 5). Shaw & Fortey (1977, Fig. 7) have shown that no Llandeilo slope deposits are preserved in North America (ibid.) and consequently there are no records of *Robergia* of that age there (cf. also Churkin 1966, text-fig. 3). Thus the Swedish upper Llandeilo/lower Caradoc species of the 'American' stock bridge the stratigraphical and morphological gap between the oldest and the younger North American forms. In due time it seems that the 'American' stock migrated from the east into the central North American basin during a period of submergence. Thence they gave rise to two evolutionary lines: one that led to the North American/northeast Siberian genus *Pugilator* (uppermost Caradoc/Ashgill), the other to the northeast Chinese *R. sinensis* (Ashgill).

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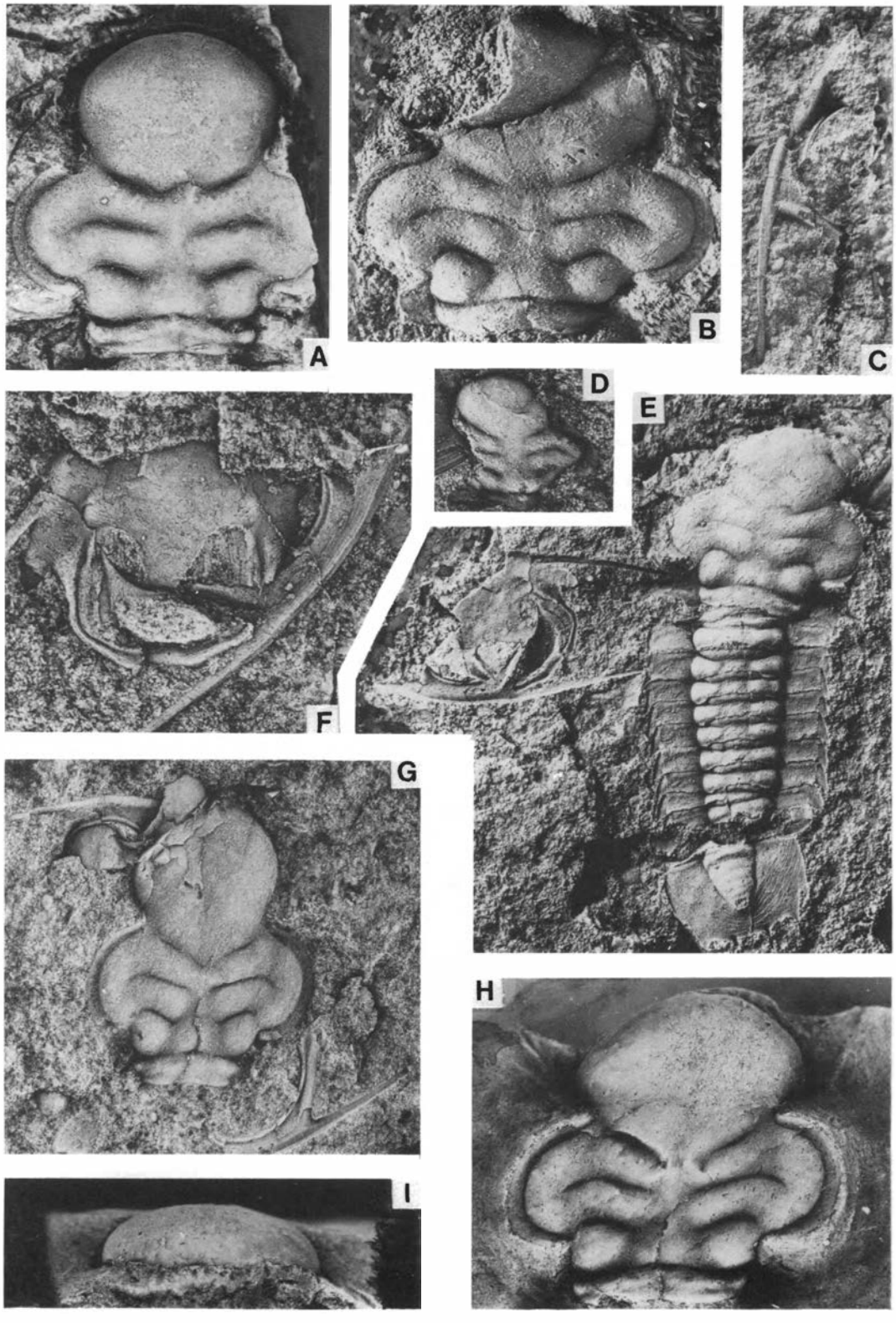

Fig. 13. A–I. *Robergia microphthalma* (Linnarsson, 1875), Andersö Shale, Sunne Sokn (community), Jämtland, Sweden. A. Dorsal view of longitudinally slightly compressed cranidium. LO 2556 t. Original of Hadding 1913, Pl. 8, fig. 15. Andersön. ×5.5. B. Dorsal view of holotype cranidium. SGU type 3952. Figured by Linnarsson 1875, Pl. 22, fig. 3; also Whittington 1950, Pl. 71, fig. 6. Önsvedsbäcken. Coll. G. Linnarsson 1871. ×8. C. Dorsal view of librigena associated with the specimens in Fig. 14C, H. SGU type 5440. Önsvedsbäcken. Coll. G. von Schmalensee 1884. ×5.5. D. Dorsal view of incomplete early holaspid cranidium. SGU type 5441. Zone of *Hustedograptus teretiusculus*. About 100 m NW of Högen. Coll. P. Thorslund 1936. ×20. E. Dorsal view of almost complete exoskeleton in moulting position. SGU type 3911. Figured by Nikolaisen 1983, Pl. 15, fig. 8. Zone of *Nemagraptus gracilis*. Frösön. Coll. P. Thorslund 1950. ×5. F. Latex cast, ventral view of lower cephalic unit of specimen Fig. 13E. SGU type 3911. Zone of *Nemagraptus gracilis*. Frösön. Coll. P. Thorslund 1950. ×9.5. G. Dorsal view of transversally slightly compressed upper cephalic unit in moulting position. SGU type 5442. Zone of *Hustedograptus teretiusculus*. Högen. Coll. P. Thorslund 1936. ×5. H–I. Dorsal and anterior view of complete but slightly distorted cranidium. SGU type 5443. Locality and horizon as for Fig. 13D. ×6.

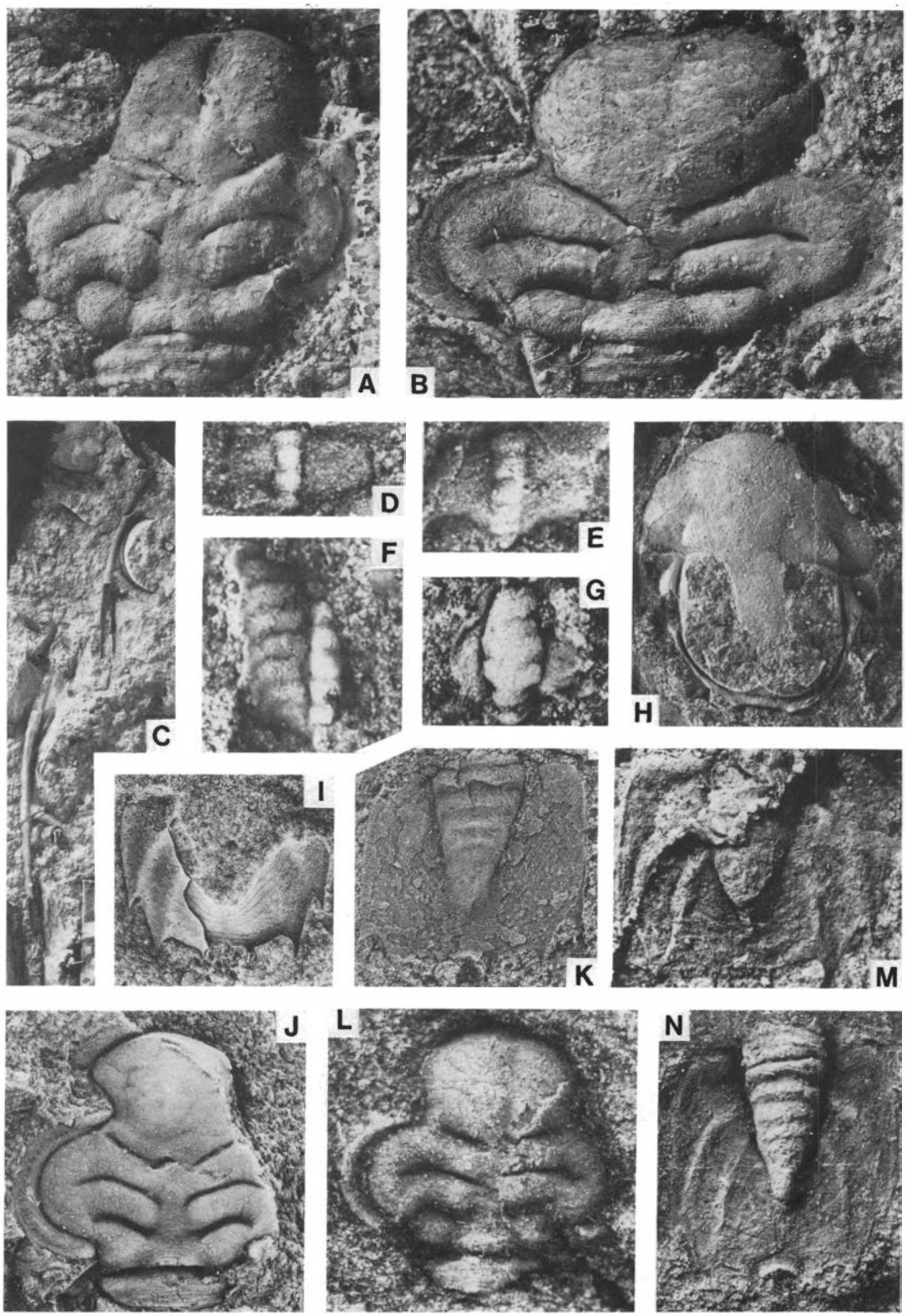

Fig. 14. A–I. *Robergia microphthalma* (Linnarsson, 1875), Andersö Shale, Sunne Sokn (community), Jämtland, Sweden. A. Latex cast, dorsal view of external mould of slightly distorted and incomplete cranidium showing prosopon. SGU type 5444. Zone of *Hustedograptus teretiusculus.* Northeastern side of Frösön. Coll. B. Asklund 1936. ×5.5. B. Latex cast, dorsal view of external mould of longitudinally compressed cranidium showing prosopon. SGU type 5445. Locality and horizon as for Fig. 14A. ×7. C. Dorsal view of two librigenae, SGU types 3958–3959, figured by Holm 1897, Pl. 8, fig. 1; 1898, Pl. 1, fig. 1; Whittington 1950, Pl. 71, fig. 1. Önsvedsbäcken. Coll. G. von Schmalensee 1884. ×3.5. D. Dorsal view of incomplete protopygidium. SGU type 5446. Zone of *Hustedograptus teretiusculus.* About 100 m NW of Högen. Coll. P. Thorslund 1936. ×27. E. Dorsal view of transitory pygidium. SGU type 5447. Locality and horizon as for Fig. 14D. ×27. F. Dorsal view of incomplete early meraspid thorax and pygidium. SGU type 5448. Locality and horizon as for Fig. 14D. ×27. G. Dorsal view of early meraspid cranidium. SGU type 5449. Locality and horizon as for Fig. 14D. ×27. H. Ventral view of almost complete, slightly distorted, hypostome associated with the specimens in Figs. 13C and 14C. SGU type 5450. Önsvedsbäcken. Coll. G. von Schmalensee 1884. ×7. I. Dorsal view of fragmentary pygidium. LO 2558 t. Figured by Hadding 1913, Pl. 8, fig. 17. Andersön. Coll. Moberg & Kullberg 1907. ×5. J. *Robergia scanica* Hadding, 1913. Holotype, dorsal view of incomplete cranidium. LO 1997 t. Figured by Moberg 1907, Pl. 1, fig. 4; Hadding 1913, Pl. 8, fig. 19. *Dicellograptus* Shale, Zone of *Hustedograptus teretiusculus.* Creek section, Röstånga Church, Scania, Sweden. Old collection. ×10. K. *Robergia sparsa* Nikolaisen, 1983. Latex cast, dorsal view of complete but flattened and poorly preserved pygidium. LO 2559 t. Figured by Hadding 1913, Pl. 8, fig. 18 as *Robergia microphthalma*?; also Whittington 1950, Pl. 71, fig. 7. Andersö, Sunne Sokn (community), Jämtland, Sweden.

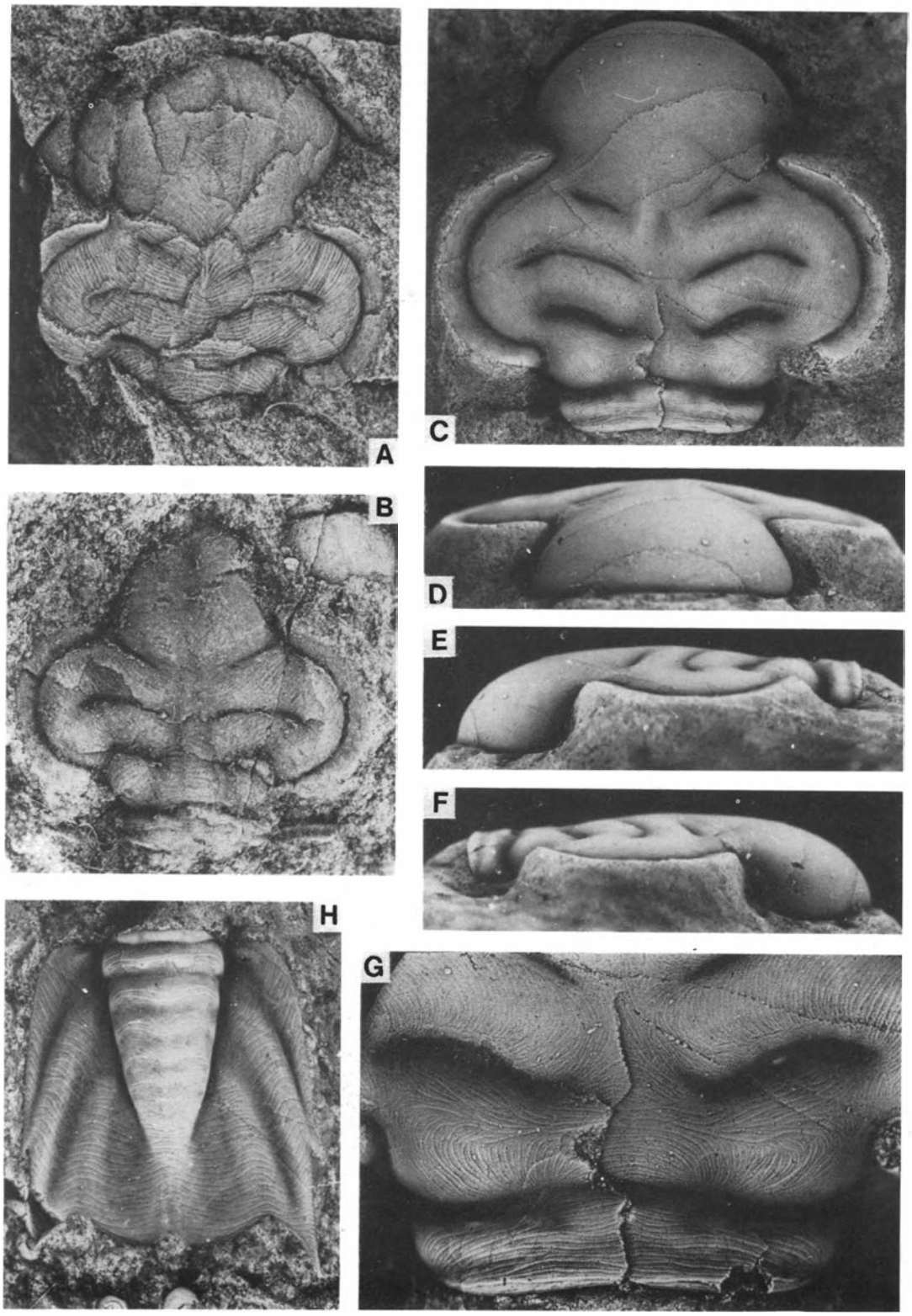

Fig. 15. A–B. *Robergia barrandii* (Etheridge & Nicholson, 1879). Lower Ardmillan Series, Balclatchie Group, Balclatchie, Girvan, Ayrshire, Scotland. Mrs. Gray collection. A. Dorsal view of crushed, slightly incomplete cranidium showing well-preserved prosopon. BM In. 21005. Figured by Reed 1903, Pl. 5, fig. 2. ×8. B. Holotype, dorsal view of incomplete cranidium. MB In. 21004. Figured by Etheridge & Nicholson 1879, Pl. 10, fig. 13; also Reed 1903, Pl. 5, fig. 1. ×11. C–H. *Robergia striatella* sp. nov. Andersö Shale, Zone of *Nemagraptus gracilis*. East of Käringnäset, northern beach of Andersön, Sunne Sokn (community), Jämtland, Sweden. Coll. P. Thorslund 1937. C–G. Paratype, dorsal, anterior, left and right lateral views, and detail of posterior part of median area and occipital ring showing the prosopon SGU type 3910. C–F ×8; G ×16. H. Holotype, dorsal view of pygidium. SGU type 3909. ×7.

Coll. A. Hadding 1912. ×6. L–N. *Robergia barrandii* (Etheridge & Nicholson, 1879). L. Dorsal view of early holaspid cranidium. MB In. 20998. Figured by Reed 1903, Pl. 5, fig. 3. Lower Ardmillan Series, Balclatchie Group, Balclatchie, Girvan, Ayrshire, Scotland. Mrs Gray collection. ×20. M. Latex cast, dorsal view of external mould of small pygidium. HM A. 18487b. Figured by Tripp 1980, Pl. 1, fig. 28. Lower Balclatchie Group. Dalfask, Girvan. ×14. N. Dorsal view of slightly distorted pygidium. BM In. 20993. Figured by Etheridge & Nicholson 1879, Pl. 14, fig. 11 as *Cheirurus*(?) sp. ind. (a); also Reed 1903, Pl. 4, fig. 9 as *Apatokephalus* sp. Locality and horizon as for Fig. 14L. ×11.

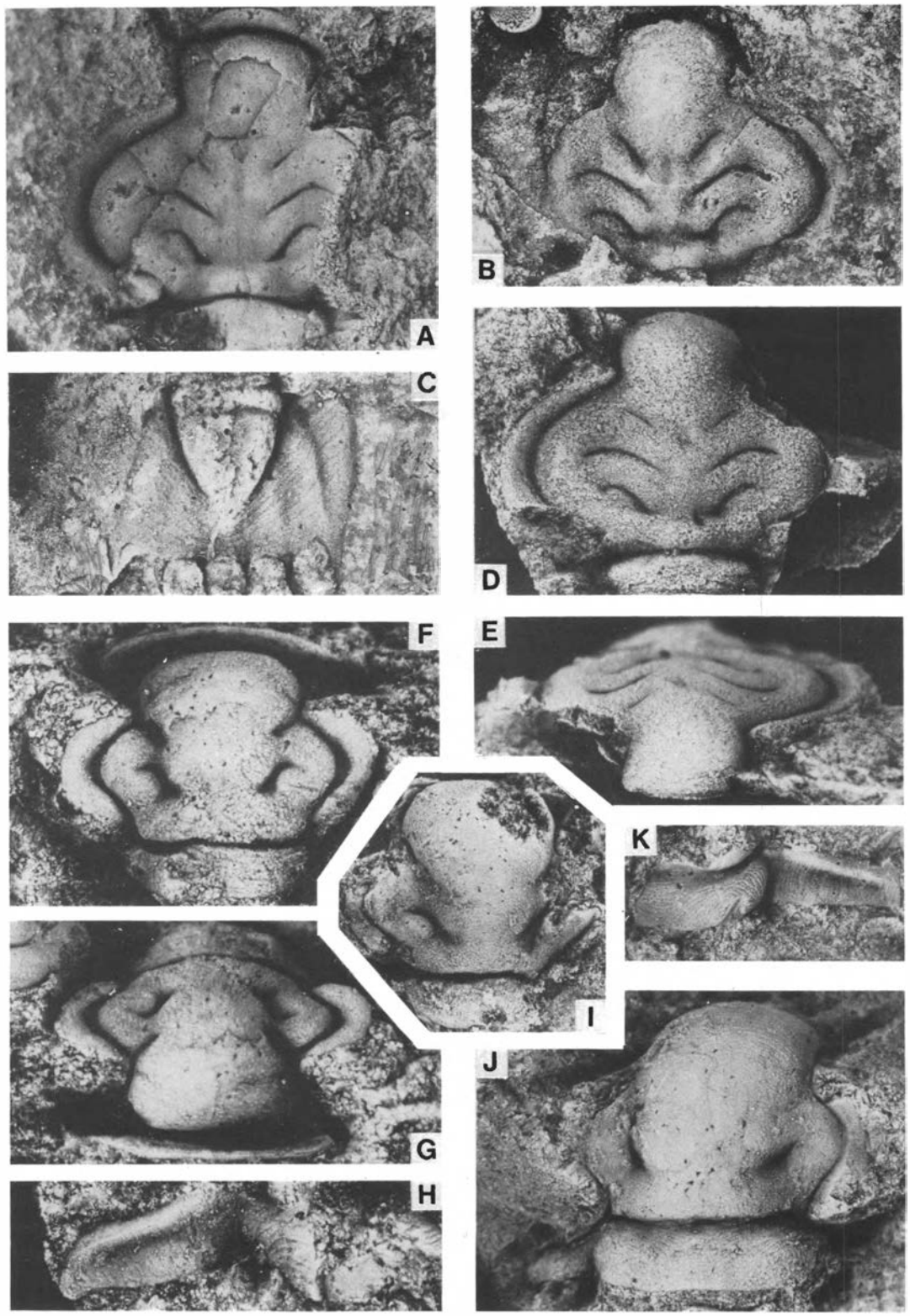

Fig. 16. A–C. *Arator mariannus mariannus* (Koroleva, 1965). Tselinograd horizon, Lidievka Formation, about 12 km east of Lidievka, Belyi Kordon, northern Kazakhstan. Coll. M. A. Zhukova. A. Holotype, dorsal view of magnesian oxychloride replica, incomplete cranidium. 1101/120 GM IGN. Figured by Koroleva 1965, Pl. 2, fig. 9; 1982, Pl. 16, fig. 7. ×10. B. Paratype, dorsal view of magnesian oxychloride replica, incomplete cranidium. 1101/121 GM IGN. Figured by Koroleva 1965, Pl. 2, fig. 10; 1982, Pl. 16, fig. 8. ×10. C. Paratype, dorsal view of magnesian oxychloride replica, almost complete pygidium. 1101/124 GM IGN. Figured by Koroleva 1965, Pl. 2, fig. 12; 1982, Pl. 16, fig. 9. ×10. D–E. *Arator mariannus* (Koroleva, 1965) *asiaticus* (Koroleva, 1982). Paratype, dorsal and dorso-anterior view of incomplete cranidium. 1101/119 GM IGN. Erkebidaik horizon, Lidievka Formation, about 12 km east of Lidievka, Belyi Kordon, northern Kazakhstan. ×12. F–K. *Eorobergia breviceps* (Raymond, 1925). Normanskill boulder, 'Mystic Conglomerate', about 3 km north of Mystic, Missisquoi County, Quebec, Canada. Coll. P. E. Raymond 1923. F–G. Holotype, dorsal and dorso-anterior views of cranidium. MCZ 1727. ×16. H. Left dorso-lateral view of topotype fragmentary thoracic tergite associated with the holotype cranidium. MCZ 1727. ×16. I. Paratype, dorsal view of fragmentary cranidium. MCZ 3276a. ×10. J. Paratype, dorsal view of incomplete, slightly distorted cranidium. MCZ 3276b. ×10. K. Right dorso-lateral view of topotype fragmentary thoracic tergite associated with the paratype cranidium in Fig. 16J. MCZ 3276c. ×10.