

THE TRILOBITE SUBFAMILY MONORAKINAE (PTERYGOMETOPIDAE)

by DAVID J. HOLLOWAY

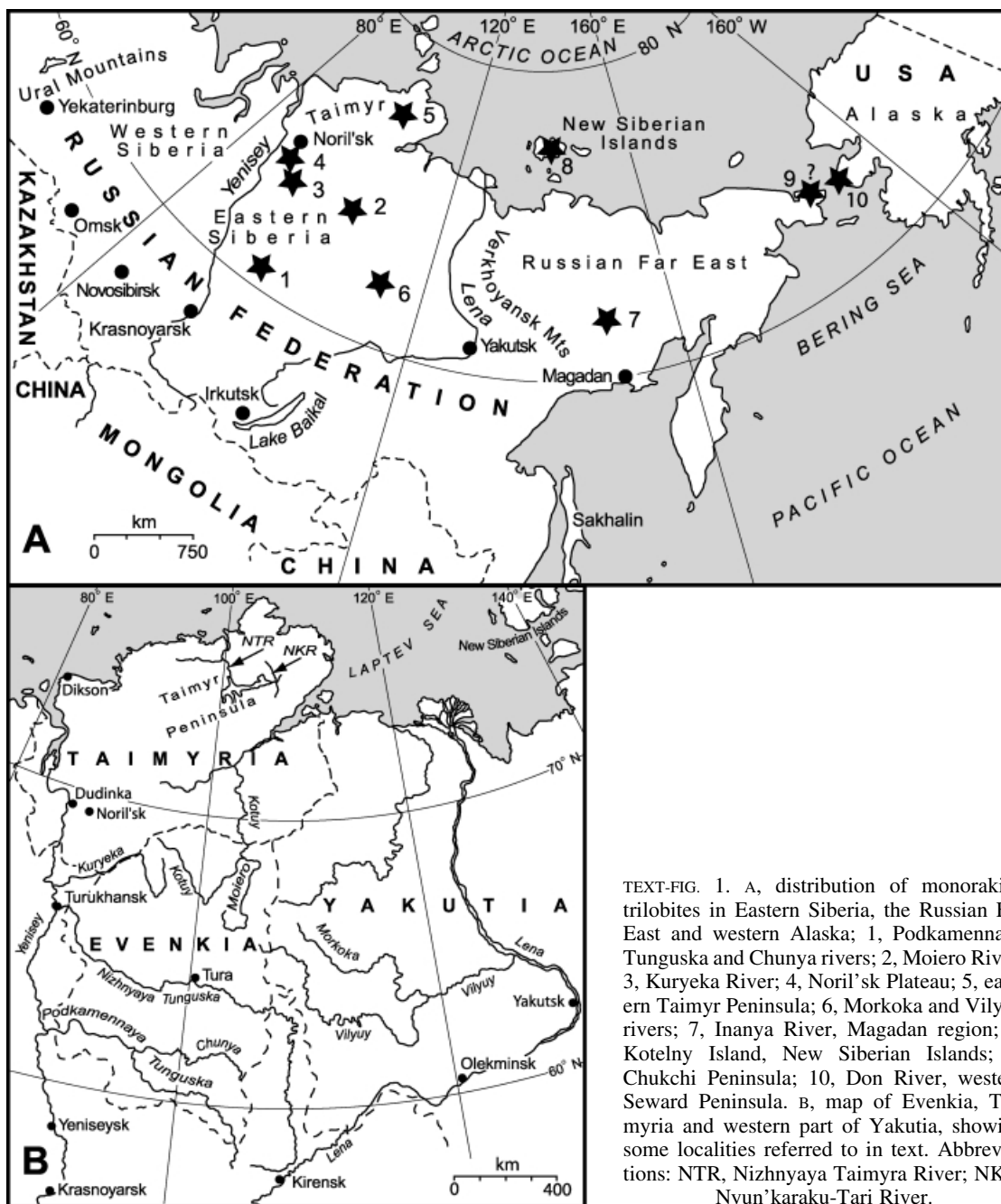
ABSTRACT. The Monorakinae is a subfamily of the Pterygometopidae characterised by the fusion of L2 and L3 in the glabella. The resulting bicomposite lobe is expanded backwards to reach the occipital furrow, displacing L1 from contact with the axial furrow and causing the realignment of S1 to a markedly oblique orientation. The bicomposite lobe is commonly bounded adaxially by a longitudinal furrow containing three pairs of apodemal pits. The Monorakinae was probably derived from the Pterygometopinae, and includes the genera and subgenera *Monorakos*, *Carinopyge*, *Ceratevenkaspis*, *Elasmaspis*, *Evenkaspis* (*Evenkaspis*) and *E.* (*Parevenkaspis*), of which *Carinopyge*, *Elasmaspis* and *Evenkaspis* (*Parevenkaspis*) are known only from limited parts of the exoskeleton. Monorakines have a stratigraphical range of Caradoc–Ashgill. Their known geographical distribution in the Siberian Platform, Taimyr, the Russian Far East, and the Seward Peninsula of Alaska is restricted to areas that in the Ordovician were part of the palaeocontinents of Siberia and Arctida, which must have been connected or situated close together at that time. The occurrence of monorakines in the Taimyr Peninsula but their absence from Baltica does not support the suggestion of some workers that Taimyr was part of Baltica in the Ordovician.

KEY WORDS: trilobites, Late Ordovician, Siberia, Monorakinae, taxonomy, palaeogeography, phylogeny.

THE Monorakinae is a small and rather poorly known subfamily of the Pterygometopidae recorded only from the Upper Ordovician (Caradoc–Ashgill) of Siberia, the Russian Far East, and western Alaska (Text-fig. 1). The greatest number of species has been described from the Podkamennaya Tunguska River and its tributaries in southern Evenkia, Eastern Siberia. Farther north, monorakines occur in the region of the Kuryeka and Moiero rivers of northern Evenkia, the Noril'sk Plateau in south-western Taimyria, and in the Taimyr Peninsula. In the Russian Far East, monorakines have been recorded from the Vilyuy and Morkoka rivers of western Yakutia, in the Inanya River basin north of Magadan, on Kotelny Island in the New Siberian Islands, and from the Chukchi (Chukotka) Peninsula. The record of monorakines from Alaska is confined to a single species from the Don River in the western part of the Seward Peninsula. Two species from the Upper Ordovician of Greenland were assigned to *Monorakos* by Troedsson (1929) but I agree with Maksimova (1962, p. 108) that the specimens belong to the eomonorachine *Calyptaulax* (see also Ormiston 1978, p. 345; Ormiston and Ross 1979, p. 55). The report of Monorakinae in the western United States by Whittington (1966, p. 720) and Whittington and Hughes (1972, p. 254) was based on *Isalaux*, a genus that does not belong to this subfamily but may be an eomonorachine (see below).

HISTORY OF CLASSIFICATION

Monorakos was proposed by Schmidt (1886), as a subgenus of *Phacops*, to include two new species from the Upper Ordovician of the Podkamennaya Tunguska River, southern Evenkia. Clarke (1894, p. 729) allied *Monorakos* with *Pterygometopus*, the latter being regarded as a subgenus of *Dalmanites*; *Monorakos* was subsequently considered to be a subgenus of *Pterygometopus* by Reed (1905, p. 228) and Kozłowski (1923, p. 32), and as an independent genus of the Pterygometopinae by Reed (1927, p. 353), Delo (1935, p. 416), Weber (1951, p. 42) and Hupé (1953, 1955). Kramarenko (1952) proposed the new subfamily Monorakeinae within the Dalmanitidae, to include *Monorakos* (of which he described several new species from the Podkamennaya Tunguska River) and the three new genera *Ceratevenkaspis*, *Evenkaspis* and *Parevenkaspis*; Maksimova (1955), however, included the Monorakeinae in the Phacopidae. Pillet (1954)



TEXT-FIG. 1. A, distribution of monorakine trilobites in Eastern Siberia, the Russian Far East and western Alaska; 1, Podkamennaya Tunguska and Chunya rivers; 2, Moiero River; 3, Kuryeka River; 4, Noril'sk Plateau; 5, eastern Taimyr Peninsula; 6, Morkoka and Vilyuy rivers; 7, Inanya River, Magadan region; 8, Kotelny Island, New Siberian Islands; 9, Chukchi Peninsula; 10, Don River, western Seward Peninsula. B, map of Evenkia, Taimyria and western part of Yakutia, showing some localities referred to in text. Abbreviations: NTR, Nizhnyaya Taimyra River; NKR, Nyun'karaku-Tari River.

added *Trypaulites* and possibly *Malladaia* (both of Devonian age) to the Monorakeinae, which he combined with the new subfamily Coronurinae [including the Devonian genera *Coronura*, *Corycephalus*, *Odontocephalus* and possibly *Anchiopsis* (= *Anchiopella*, *sensu* Pillet)] in the Family Monorakeidae. The Monorakeinae was distinguished mainly by the absence of marginal spines on the cephalon and pygidium, and the reduction of the lateral glabellar furrows to pits in the longitudinal furrow, whereas the

Coronurinae was characterised by marginal cephalic and pygidial spines, and by a narrow, rectangular glabella. *Trypaulites*, *Malladaia* and the Coronurinae were excluded from the Monorakidae by Struve (1959), who added *Isalaux* Frederickson and Pollack, 1952 to the family, in which he recognised no subfamilial divisions. The classification of the family adopted by Kramarenko and Maksimova (1960) was similar to that of Struve, except that they added *Carinopyge* Maksimova, 1955 (originally placed in the Pterygometopinae) and did not include *Isalaux*, which they placed instead in the Pterygometopidae. Balashova (1960*a,b*) divided the Monorakeidae into the Monorakeinae, Carinopyginae and Elasmaspisinae, the last two subfamilies being newly proposed in her 1960*a* publication (the name of the Elasmaspisinae was invalidly emended to Elasmaspiinae in her 1960*b* publication). To the Monorakeinae she assigned *Monorakos*, *Ceratevenkaspis*, *Evenkaspis*, *Parevenkaspis* and *Trypaulites*, whereas in the Carinopyginae she included *Carinopyge* and *Anchiopsis*; the Elasmaspisinae included only *Elasmaspis* Kramarenko, 1956. Balashova's classification was not adopted by later authors (e.g. Maksimova 1962; Semenova 1978, 1984), most of whom followed the arrangement of Kramarenko and Maksimova (1960). Ludvigsen and Chatterton (1982), however, considered the Monorakinae to be a subfamily of the Pterygometopidae, and their classification is accepted herein.

PALAEOGEOGRAPHICAL IMPLICATIONS

Ormiston and Ross (1979) considered that the distribution of monorakines suggested the existence in the Ordovician of a unified Siberia-Kolyma continent that also included the Seward Peninsula of Alaska. However, the Kolyma-Omolon region of the Russian Far East, previously interpreted by some workers as the core of a discrete 'Kolyma plate', is now recognized as a complex mosaic of accreted terranes of both oceanic and continental origins, and was not a single entity in the Ordovician (Andrews-Speed 1981; Zonenshain *et al.* 1990).

The Siberian plate, bounded by the Ural Fold Belt in the west and the Verkhoyansk-Kolyma Fold Belt in the east, occupied equatorial latitudes during the Ordovician and was geographically inverted north to south with respect to its present orientation (Torsvik 1998, figs 1–4). In most palaeocontinental reconstructions for the middle–late Ordovician (e.g. Scotese and McKerrow 1990, figs 8–9; Torsvik *et al.* 1995, fig. 10) Siberia is shown to include Taimyr, but Zonenshain *et al.* (1990, figs 118–119) considered the northern part of the Taimyr Peninsula to be part of a separate plate, called Arctida, which also encompassed a number of other now disparate continental fragments, namely Severnaya Zemlya, the New Siberian and Wrangel islands, the Chukchi Peninsula, the Seward Peninsula and Brooks Range of Alaska, and the northern parts of Ellesmere Island and Greenland. Yet a different view on the palaeogeographical position of Taimyr was presented by Cocks and Modzalevskaya (1997) and Cocks and Fortey (1998), who argued on the basis of Ashgill brachiopod faunas that it was part of Baltica in the Ordovician (see also Torsvik 1998, p. 109, fig. 1).

The occurrence of monorakines in the Taimyr Peninsula, the New Siberian Islands and the Seward Peninsula, and the unverified report of *Monorakos* from the Chukchi Peninsula by Oradovskaya (*in* Zanina and Likharev 1975; see below), lend support to the concept of Arctida presented by Zonenshain *et al.* (1990). Other occurrences of monorakines are restricted to Siberia, or to areas that were part of the Siberian plate in the Ordovician. The occurrence of *Ceratevenkaspis* sp. (= '*Monorakos mutabilis* Kramarenko' of Chugaeva 1964, 1968; see below, and Pl. 3, fig. 12) in the Inanya River basin of the Magadan Region, east of the present margin of the Siberian plate, is in sediments considered by Zonenshain *et al.* (1990, pp. 121, 124) to have been deposited on the eastern edge of the Siberian continent and rifted from it in the Late Devonian. The distribution of monorakines thus suggests that Arctida may have formed part of the Siberian continent in the Late Ordovician, or was situated close enough to it to be in faunal contact. The occurrence of monorakines in Taimyr but their absence from Baltica does not support the view of Cocks and Modzalevskaya (1997) and Cocks and Fortey (1998) that Taimyr was part of Baltica in the Ordovician.

SYSTEMATIC PALAEONTOLOGY

Terminology. Morphological terminology follows Whittington and Kelly (1997), with the addition of the abbreviations A0, A1, A2 and A3 to denote the apodemes or apodemal pits associated with the occipital furrow and glabellar furrows S1–S3 respectively. Stratigraphical terminology and correlation of the Russian sequences follows Ross and Talent (1988), and the series subdivisions of the Ordovician follow Fortey *et al.* (1995, 2000).

Family PTERYGOMETOPIDAE Reed, 1905

Remarks. The diagnosis of the family given by Ludvigsen and Chatterton (1982, p. 2182) incorrectly refers to distinct interpleural and faint pleural furrows in the pygidium; it is the pleural furrows that are well developed and the interpleural furrows that are weak, as reported by Ludvigsen and Chatterton everywhere else in their paper. To Ludvigsen and Chatterton's diagnosis should be added the fact that the pygidial interpleural furrows in the Pterygometopidae are deflected strongly backwards distally to converge with the distal end of the succeeding pleural furrow.

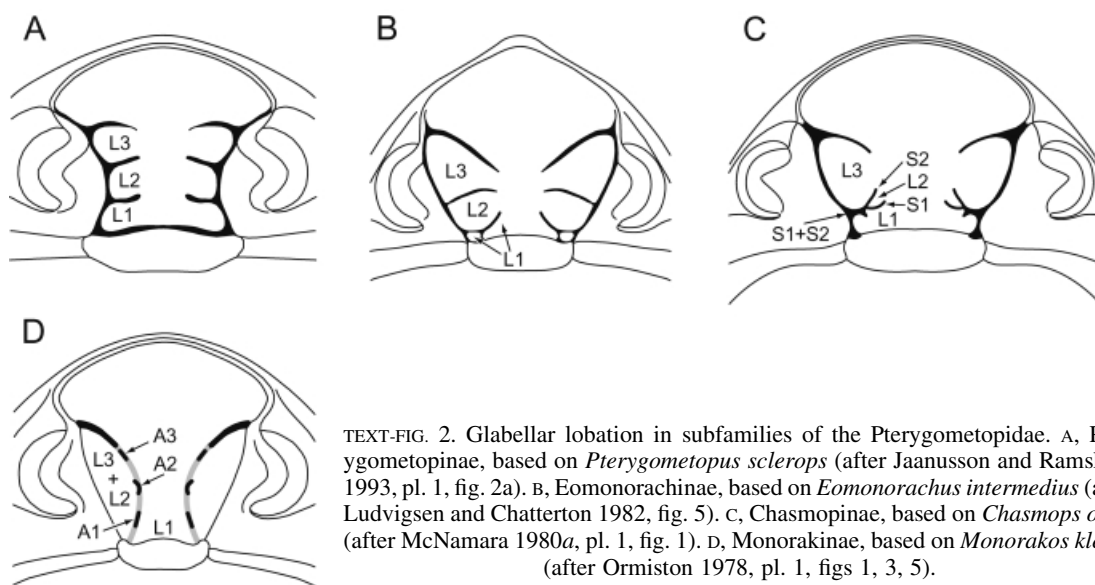
Ludvigsen and Chatterton's (1982) four-fold subdivision of the Pterygometopidae into the Pterygometopinae, Chasmopinae, Eomonorachinae and Monorakinae is accepted here. Each of these subfamilies is characterised by a distinctive type of glabellar segmentation (Text-fig. 2). The most primitive type is present in members of the Pterygometopinae (see Ludvigsen and Chatterton 1982; Jaanusson and Ramsköld 1993), which have all of the lateral glabellar furrows well developed, L1 and L2 approximately equal in length (exsag.), and L3 expanding only weakly or moderately abaxially. In the other subfamilies, the glabellar segmentation has been modified by changes in the relative sizes of certain lateral lobes, some of which may be displaced by other lobes, and by the partial or complete effacement, or fusion, of S1 and/or S2. In the Eomonorachinae (Ludvigsen and Chatterton 1982), L1 is reduced in length (exsag.) in comparison to L2, and has well-developed lateral nodes; S2 is weak or effaced abaxially, so that L2 and L3 are partially confluent; and L3 expands rather strongly abaxially. In the Chasmopinae (McNamara 1980*a, b*), L3 is greatly enlarged due to its backwards expansion, displacing L2 and in some genera also the anterior part of L1 from contact with the axial furrow; S1 and S2 are fused abaxially; and L2 is reduced to a tiny swelling at the intersection of the narrow (tr.), adaxial portions of S1 and S2. In the Monorakinae, S2 is effaced (except on the median part of the glabella in *Elasmaspis*), its former position being indicated adaxially by apodemal pit A2; the bicomposite lobe formed by the fusion of L2 and L3 is expanded backwards to displace the abaxial part of L1 (see below); and S1 (if impressed) is markedly oblique, joining apodemal pit A1 to the outer end of the occipital furrow.

Subfamily MONORAKINAE Kramarenko, 1952

[*nom. correct.* Struve, 1959, *ex* Monorakeinae Kramarenko, 1952. Subjective synonyms:
Carinopyginae Balashova, 1960*a*; Elasmaspisinae Balashova, 1960*a*;
Elasmaspiinae Balashova, 1960*b* (unjustified emendation)]

Diagnosis. Glabella expanding forwards from occipital furrow. L2 and L3 fused in bicomposite lobe that extends backwards to reach occipital furrow, displacing abaxial part of L1; bicomposite lobe generally bounded adaxially by arcuate longitudinal furrow joining S3 and S1. S1 (if impressed) directed obliquely outwards and backwards to meet outer part of occipital furrow; median part of L2 between longitudinal furrows commonly depressed. Three pairs of apodemal pits (not identified in *Elasmaspis*) present adaxial to bicomposite lobe: A1 and A3 slit-like or nearly circular, A2 circular or crescentic. Genal spine generally present [absent in *Elasmaspis* and *Evenkaspis* (*Parevenkaspis*)], slender and rounded in cross section or broad, flattened and bearing an extension of lateral border furrow. Pygidium triangular to parabolic in outline, with or without lateral border and mucro.

Genera and subgenera included. *Monorakos* Schmidt, 1886; *Carinopyge* Maksimova, 1955; *Ceratevenkaspis* Kramarenko, 1952; *Elasmaspis* Kramarenko, 1956; *Evenkaspis* (*Evenkaspis*) Kramarenko, 1952; *E. (Parevenkaspis)* Kramarenko, 1952.



TEXT-FIG. 2. Glabellar lobation in subfamilies of the Pterygomtopidae. A, Pterygomtopinae, based on *Pterygomtopus sclerops* (after Jaanusson and Ramsköld 1993, pl. 1, fig. 2a). B, Eomonorachinae, based on *Eomonorachus intermedius* (after Ludvigsen and Chatterton 1982, fig. 5). C, Chasmopinae, based on *Chasmops odini* (after McNamara 1980a, pl. 1, fig. 1). D, Monorakinae, based on *Monorakos kledos* (after Ormiston 1978, pl. 1, figs 1, 3, 5).

Remarks. Though he did not specifically discuss the homology of the single pair of large lateral glabellar lobes in *Monorakos*, Schmidt (1886, pp. 506, 508) compared the glabellar structure to that of *Chasmops*, which is characterised by an enlarged L3. Most other authors (e.g. Kramarenko 1952, p. 401; Hupé 1955, p. 254; Struve 1959, p. 493; Kramarenko and Maksimova 1960, p. 169; Ormiston 1978, p. 350; Ludvigsen and Chatterton 1982, p. 2202) have considered the composite lobe of monorakines to be composed of L2 and L3, an interpretation with which I am in agreement. It could be argued, however, that the composite lobe includes L1 as well as L2 and L3. This was apparently the view of Balashova (1960a, p. 7; 1960b, p. 59), who stated that in typical monorakines all three lateral glabellar lobes are merged in one elongated, convex lobe. If this were the case, then the oblique furrow joining apodemal pit A1 to the outer part of the occipital furrow would not be S1, which must be effaced, but a continuation of the longitudinal furrow running adaxial to L1. In the absence of knowledge of the early ontogeny of monorakines the homology of this oblique furrow cannot be determined with certainty. However, the fact that the furrow is aligned in the same direction as A1 (in forms having a linear rather than subcircular A1; e.g. Pl. 1, figs 2, 4, 7, 10–11; Pl. 4, figs 9, 17; Pl. 5, figs 1–2, 5–6) suggests that the furrow is S1 rather than an extension of the longitudinal furrow. Hence L1 has been displaced from contact with the axial furrow by backward expansion of the bicomposite lobe formed by the fusion of L2 and L3.

Whether the backward expansion of the bicomposite lobe results mainly from elongation of L2 or L3, or both, is uncertain because the anterior extent of L2 cannot be determined, S2 being completely effaced abaxial to apodemal pit A2. However, the fact that A2 is commonly directed obliquely forwards and outwards (e.g. Ormiston 1978, pl. 1, figs 1, 3, 8–9; Pl. 1, figs 1–2, 11; Pl. 2, fig. 9; Pl. 4, fig. 9; Pl. 5, figs 1, 5), whereas S1 is directed strongly posterolaterally, suggests that the elongation mainly involves L2. The approximately equal exsagittal spacing of apodemal pits A0–A3 at their adaxial ends indicates that elongation of the lateral glabellar lobes has not involved the adaxial parts of L2 and L3. Adaxial to the bicomposite lobes, the median glabellar lobe between the front of A1 and the level of A2 (i.e. median part of L2) is commonly depressed and may lack tuberculate sculpture like that on the remainder of the glabella (e.g. Ormiston 1978, pl. 1, figs 1, 3, 8–9; Pl. 3, figs 1, 4; Pl. 4, figs 6–7; Pl. 5, figs 1–2, 5, 16). Behind this depressed region, L1 is differentiated as a slightly inflated band adaxial to S1 (if impressed).

The frontal lobe of the glabella in some monorakines is not bounded laterally on the cranidium by the axial and preglabellar furrows, but appears to extend across the facial suture to incorporate a narrow (tr.), slightly inflated, crescentic region on the librigena [e.g. *Monorakos kledos*, see Ormiston 1978, pl. 1, figs

4–5; *Evenkaspis (Evenkaspis) galeata*, Pl. 4, figs 6, 9; *E. (E.) nikiforovae*, Pl. 5, figs 16, 18]. This phenomenon is also characteristic of some genera of Pterygometopinae, including *Achatella*, *Estoniops* and *Keilapyge* (see Ludvigsen and Chatterton 1982, pl. 1, figs 2, 4, 7; Jaanusson and Ramsköld 1993, pl. 2, figs 2–3; pl. 4, figs 1, 3; pl. 5, figs 3–4). In these Pterygometopinae, the inflated, crescentic or subtriangular region on the front of the librigena adjacent to the facial suture was termed the ‘transsutural wing’ by Jaanusson and Ramsköld, who recognised (1993, p. 746) that it is not homologous with any part of the true frontal lobe, though they regarded it as part of the frontal lobe for descriptive purposes. The extent to which transsutural wings are present in the Monorakinae, and the usefulness of this character in determining relationships within the subfamily, are uncertain at present, because the majority of species are known only from incomplete and poorly preserved specimens lacking the librigenae. However, transsutural wings are not present in all species of *Monorakos* and *Evenkaspis*, because on cranidia of *M. ossacrum* (Pl. 2, fig. 9), *M. planus* (Pl. 1, figs 3, 6), and ‘*Evenkaspis galeata*’ of Maksimova (1962, p. 124, pl. 15, figs 4–5) (see Pl. 4, fig. 17) the frontal lobe is bounded abaxially by shallow but distinct axial and prelabellar furrows.

Monorakine hypostomes are known in *Monorakos ossacrum* (Pl. 2, fig. 5), *M. kledos* (Ormiston 1978, pl. 1, fig. 11) and *Carinopyge? spinifera* (Balashova 1960a, b, pl. 4, fig. 18c; Pl. 2, fig. 4). The hypostome of *M. ossacrum* resembles those of Eomonorachinae (see Ludvigsen and Chatterton 1982) and Chasmodipinae (see Haller 1973; Röömusoks 1998) in having prominent shoulders and an elongated, tongue-shaped posterior border. The posterior border is broken off in the only illustrated hypostome of *M. kledos*, but the specimen is otherwise similar to *M. ossacrum*. The only known hypostome of *C.? spinifera* is too incomplete for comparison.

Isalaux, a genus that has been regarded as a monorakine (Struve 1959), was proposed by Frederickson and Pollack (1952) for their new species *I. canonensis*, based on a single enrolled and crushed dorsal exoskeleton from the Harding Sandstone (Rocklandian–Kirkfieldian, Caradoc) of Colorado. Although *I. canonensis* resembles members of the Monorakinae in having S1 joining the occipital furrow distally, it differs in the presence of a deep, transverse S2, and in the possible development of a tiny, poorly defined lateral node on L1. In the development and orientation of S1–S3, and the shape of the glabella that is not greatly expanded across L3, *Isalaux* is similar to some Eomonorachinae, especially *Eomonorachus*. I consider that *Isalaux* is most likely an eomonorachine, possibly derived from *Eomonorachus* by extreme reduction in length (exsag.) of L1, but additional, better preserved material of the type species is required to assess the affinities of the genus more reliably. Two species from the Caradoc of Eastern Siberia have been assigned to *Isalaux*, namely *I. bifolia* Maksimova, 1955, and *I. stricta* Maksimova, 1962; the latter was designated type species of the new subgenus *I. (Isalauxina)* by Maksimova (1962, p. 104), who distinguished it from the nominotypical subgenus mainly by the more distinct longitudinal furrow and the more rounded outline of the lateral glabellar lobes. Illustrated specimens of the Siberian species are small and rather poorly preserved, but at least some of the specimens that have been assigned to *stricta* appear to belong to *Eomonorachus* (e.g. Kanygin *et al.* 1977, pl. 6, figs 8–9; Semenova 1984, pl. 28, figs 4–5).

Genus MONORAKOS Schmidt, 1886

[Objective synonym: *Monorachus* Clarke, 1894 (unjustified emendation)]

Plate 1, figures 1–12; Plate 2, figs 1–3, 5, 9

Type species. Subsequent designation of Vogdes 1925, p. 106; *Phacops (Monorakos) Lopatini* Schmidt, 1886, p. 506, from the lower part of the Mangazeya Formation (Chertovskian Horizon, *Nemagraptus gracilis* Biozone, lower Caradoc), Podkamennaya Tunguska River, southern Evenkia. Syntypes include CNIGR 1/11450, small dorsal exoskeleton with partly disarticulated thorax (Schmidt 1886, pl. 30, fig. 6; Pl. 1, fig. 7 herein); CNIGR 2/11450, cranidium (Schmidt 1886, pl. 30, fig. 7; Pl. 1, fig. 11 herein); CNIGR 3/11450, small articulated dorsal exoskeleton (Schmidt 1886, pl. 30, fig. 8; Pl. 1, fig. 10 herein); and CNIGR 4/11450, pygidium (Schmidt 1886, pl. 30, fig. 9; Pl. 1, fig. 12 herein); other small and mostly disarticulated specimens are present on the same pieces of rock as the figured syntypes.

Other species. *M. consimilis* Semenova, 1978; *M. kledos* Ormiston, 1978; *M. magnus* Kramarenko, 1952; *M. morkokensis* Maksimova, 1962; *M. mutabilis* Kramarenko, 1952 (possibly a junior synonym of *M. lopatini*);

M. ossacrum Kramarenko, 1952; *M. planiusculus* Kramarenko, 1957; *M. planus* Kramarenko, 1957; *M. tunguskaensis* Kramarenko, 1952 (= *M. lopatini*; see Maksimova 1962, p. 108).

Diagnosis. Glabella narrower than cheek posteriorly, expanding strongly and rather uniformly forwards in front of occipital ring, width across frontal lobe 1.8–2.6 times width at occipital ring. Glabellar sculpture smooth, finely or coarsely granulose, or weakly tuberculate. Lateral border flattened, with sharply reflexed outer edge; genal spine broad, flattened in cross section, with longitudinal furrow extending almost its entire length. Pleural tips on posterior thoracic segments deflected strongly backwards. Pygidium multisegmented, subtriangular in outline, non-mucronate; axis narrower than pleurae anteriorly; pleurae with concave border.

Remarks. The change in spelling of the generic name to *Monorachus* by Clarke (1894, p. 729) is demonstrably intentional, as both the original and altered spellings were cited, the latter being followed by the abbreviation ‘emend.’ As an unjustified emendation in terms of the ICZN Code, *Monorachus* is an available name and is a junior objective synonym of *Monorakos* (Article 33.2.3). The change in spelling to *Monorhachis* by Vogdes (1925, p. 106) is not demonstrably intentional (the name of the type species was also misspelt by Vogdes); hence it is to be regarded as an incorrect subsequent spelling and is not an available name (Article 33.3). The listing by Kozłowski (1923, table on p. 32) of *M. lopatini* as ‘representative species’ of *Monorakos* does not constitute a valid designation of type species (Article 67.5).

Kramarenko (1952, p. 402) stated in his generic diagnosis (repeated with slight modification in Kramarenko 1957, p. 49, and in Kramarenko and Maksimova 1960, p. 169; see also Maksimova 1962, p. 107) that the cephalon and pygidium of *Monorakos* are flattened and the genal spines are small. However, the specimens available to him have all been compressed tectonically, and the genal spines are incomplete or not preserved at all. In the undeformed material of *M. kledos*, from the Ashgill (Dutro 1982) of Alaska, the cephalon and pygidium are quite strongly convex, and the genal spine is long, broad and blade-like, with a longitudinal furrow extending virtually its entire length (see Ormiston 1978, pl. 1, figs 1–12).

Oradovskaya (in Zanina and Likharev 1975, p. 189) recorded *Monorakos* sp. from the Isseten Formation (upper Llanvirn–lower Caradoc) of the Chukchi (Chukotka) Peninsula, this being the most easterly reported occurrence of monorakines in Russia. However, Oradovskaya’s identification cannot be verified as the material has not been described or illustrated.

Stratigraphical range and distribution. Caradoc–Ashgill; Eastern Siberia (Evenkia, Taimyr), Russian Far East (Yakutia, Chukchi Peninsula?), Alaska (Seward Peninsula).

Genus CARINOPYGE Maksimova, 1955

Plate 2, figures 4?, 6?, 7, 8?, 10–15

Type species. Original designation; *Carinopyge fracta* Maksimova, 1955, p. 132, from the upper part of the Mangazeya Formation (Baksanian Horizon, *Diplograptus multidens*–*Dicranograptus clingani* biozones, Caradoc) of the Rybopuchaya River, a tributary of the Chunya River, southern Evenkia. Lectotype, designated Maksimova (1962, p. 130) by use of the term ‘type specimen’ (see ICZN Article 74.5), pygidium CNIGR 654/9202; figured Maksimova (1955, pl. 31, fig. 3; 1962, pl. 16, fig. 7), Plate 2, figures 10, 12 herein.

Other species. *C. abscisa* Maksimova, 1955; *C.? ensifera* Maksimova, 1955; *C.? spinifera* Balashova, 1960a; *C.? tungusella* Semenova, 1978.

Diagnosis. Pygidium multisegmented, triangular in outline, with broad, concave border comprising 27–33 per cent sagittal pygidial length (excluding mucro, if present). Axis narrower than pleurae anteriorly, extending backwards almost to inner edge of border; prominent postaxial ridge extends across entire border. Pleural furrows short (exsag.), shallow, dying out at or just beyond inner edge of border; interpleural furrows faint on pleural field, more distinct on border; pleural ribs flattened and imbricated in cross-section. Exoskeleton minutely and densely pitted on pleural field, smooth on border.

Remarks. The illustrated specimens of the type species consist of three large, incomplete pygidia (Maksimova 1962, pl. 16, figs 6–8). The most complete of these is the lectotype (Pl. 2, figs 10–12), which preserves all of the axis, including the articulating half ring, as well as most of the left posterolateral pleural margin and part of the right; however, the posterior extremity is broken off, so it is not possible to determine whether a mucro was present. In the other two pygidia the margins are not preserved at all. The lectotype has seven rings in the apodemal sector of the axis (comprising about the anterior 60 per cent of the axis) and eight pleural furrows, the last two very faint. No rings can be discerned in the post-apodemal sector of the axis in the lectotype, but one of the other specimens (Pl. 2, fig. 14) has ten rings in the post-apodemal sector, the last few rings being distinguished by very short (exsag.), narrow (tr.) paired ridges. The third specimen (Pl. 2, fig. 15), the largest, has evidence of eight rings in the apodemal sector of the axis, six rings in the post-apodemal sector, and ten pleural furrows. The concave border expands backwards in the lectotype, comprising 33 per cent of the pygidial length sagittally (excluding mucro, if present); in the largest specimen the border is more markedly concave than in the other two. The postaxial ridge is wider (tr.) and less angular in transverse section in the lectotype than in the other specimens.

The only other species here assigned to *Carinopyge* with confidence is *C. abscisa*, based on three pygidia (only one of which has been illustrated; Maksimova 1955, pl. 30, fig. 4; 1962, pl. 16, fig. 3; Pl. 2, figs 11, 13 herein), from the upper part of the Mangazeya Formation (Baksanian Horizon, Caradoc) of the Podkamennaya Tunguska and Chunya rivers of southern Evenkia, and the Morkoka River of western Yakutia. Additional specimens, mostly from the overlying Dolbor Formation (Dolborian Horizon, uppermost Caradoc–lowermost Ashgill), were illustrated by Semenova (1978, p. 101, pl. 18, fig. 7, pl. 19, fig. 4; 1984, p. 82, pl. 35, figs 1–3) and include an incomplete dorsal exoskeleton. In the lectotype pygidium of *abscisa* the posterior extremity is broken, but other specimens (Semenova 1978, pl. 18, fig. 7; 1984, pl. 35, figs 2–3) show that the extremity is pointed and lacks a mucro.

Pygidia of *Carinopyge* are similar to those of *Monorakos* in the relatively large number of axial rings and pleural furrows, the axis that is narrower than the pleurae anteriorly, and the presence of a concave border. Pygidia of *Carinopyge* differ from those of *Monorakos* in that the border is much wider, the interpleural furrows extend much farther abaxially than the pleural furrows, and there is a prominent postaxial ridge; in addition, in *Carinopyge* the pleural furrows seem to be shallower and the pleural ribs more flattened and imbricate in longitudinal profile. The cephalon of *Carinopyge* is known with certainty only in the incomplete dorsal exoskeleton of *C. abscisa* illustrated by Semenova (1984, pl. 35, fig. 3; see above). In this specimen the cephalon is very poorly preserved, but it resembles the cephalon of

EXPLANATION OF PLATE I

All specimens are from the Mangazeya Formation (Caradoc) of the Podkamennaya Tunguska River, Evenkia; all photographs except the lower part of 5 and 10 are of plaster replicas.

Figs 1, 4. *Monorakos planiusculus* Kramarenko, 1957. 1, PIN 589/1186, cranidium, holotype, dorsal view; $\times 2.5$. 4, PIN 589/1187, cranidium, paratype, dorsal view; $\times 3$.

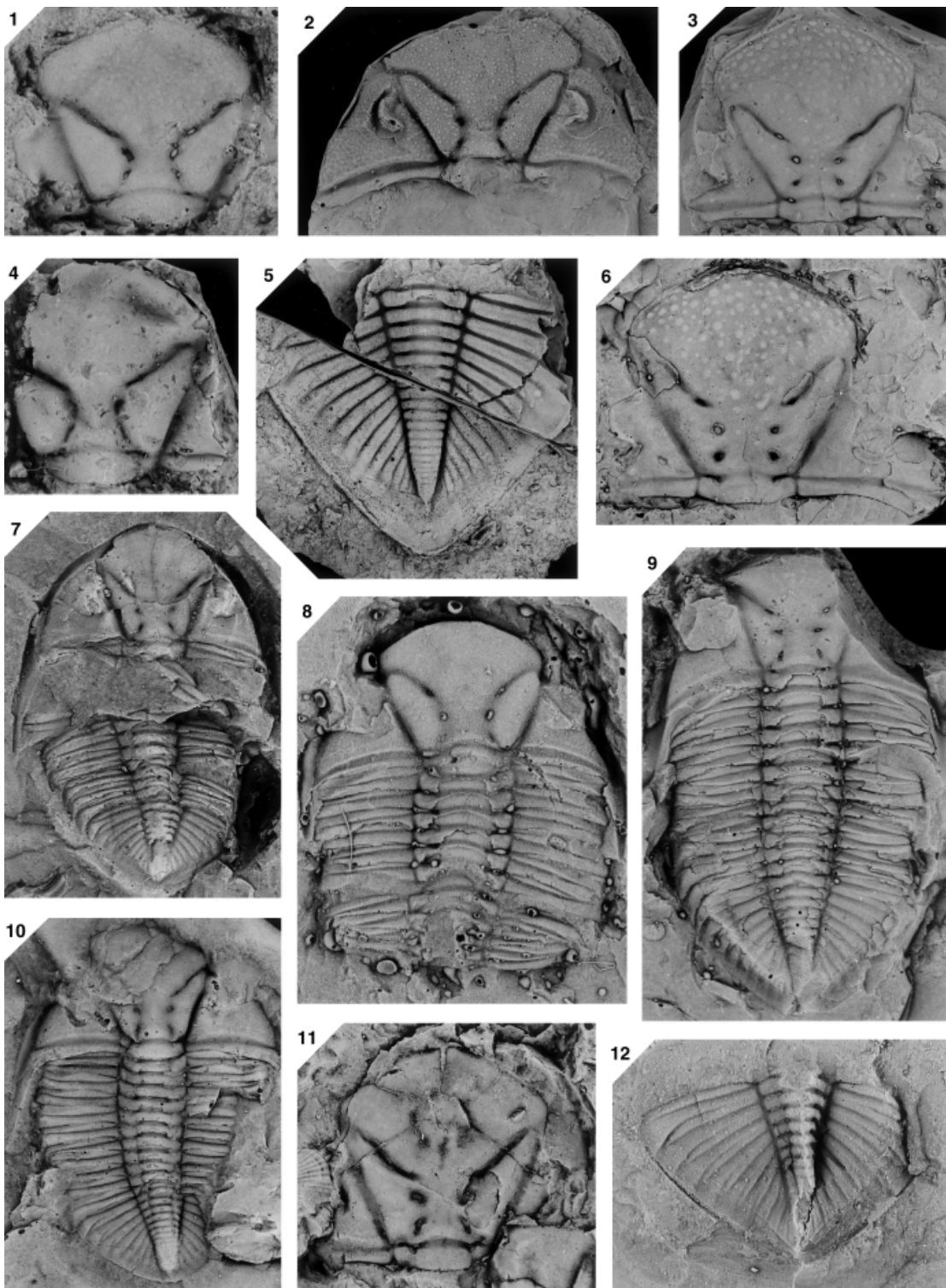
Figs 2, 5. *Monorakos magnus* Kramarenko, 1952. 2, PIN 589/1002, cranidium, holotype, dorsal view; $\times 1.75$. 5, PIN 589/1372 (lower part) and PIN 589/1002 (upper part); composite photograph of paratype pygidium broken into two parts, lower part latex cast of external mould, upper part internal mould on same slab as holotype cranidium; dorsal views; $\times 1.5$.

Figs 3, 6. *Monorakos planus* Kramarenko, 1957. 3, PIN 589/1358, cranidium, holotype, dorsal view; $\times 2$. 6, PIN 589/1357, cranidium, paratype, dorsal view; $\times 1.5$.

Figs 7, 10–12. *Monorakos lopatini* (Schmidt, 1886), syntypes. 7, CNIGR 1/11450, partly disarticulated small dorsal exoskeleton, dorsal view; $\times 5$. 10, CNIGR 3/11450, latex cast of small dorsal exoskeleton, dorsal view; $\times 5$. 11, CNIGR 2/11450, cranidium, dorsal view; $\times 2.75$. 12, CNIGR 4/11450, pygidium, dorsal view; $\times 4.5$.

Fig. 8. *Monorakos mutabilis* Kramarenko, 1952. PIN 589/1001, cranidium and incomplete thorax, holotype, dorsal view; $\times 4.5$.

Fig. 9. *Monorakos tunguskaensis* Kramarenko, 1952. PIN 589/1006, dorsal exoskeleton, holotype, dorsal view; $\times 3.5$.



HOLLOWAY, *Monorakos*

Monorakos in that the glabella is narrower than the cheeks posteriorly and expands strongly forward. As the cephalon of *Carinopyge* is so poorly known, the generic diagnosis above is based only on pygidial characters.

Other species previously assigned to *Carinopyge*, but here included in the genus with question, are *C.?* *ensifera* (Pl. 2, fig. 7) from the Caradoc of Evenkia, *C.?* *spinifera* (Pl. 2, figs 4, 6) from the Caradoc of Taimyr, and *C.?* *tungusella* (see Semenova 1978, pl. 18, fig. 8; pl. 19, fig. 8) from the uppermost Caradoc–lowermost Ashgill of Evenkia. Pygidia of these species differ from those of *fracta* and *abscisa*, amongst other features, in lacking a greatly expanded concave border and prominent postaxial ridge, and in having the pleural furrows extending as far distally as the interpleural furrows. The cephalon is known in *C.?* *spinifera* (see Balashova 1960b, pl. 4, fig. 18; Semenova 1984, pl. 35, fig. 4) and has a narrow anterior process that, although incomplete in the two specimens, was clearly rather long.

Stratigraphical range and distribution. Caradoc–lower Ashgill; Eastern Siberia (Evenkia, Taimyr?), Russian Far East (Yakutia).

Genus CERATEVENKASPIS Kramarenko, 1952

Plate 3, figures 1–12

Type species. Monotypy; *Ceratevenkaspis armata* Kramarenko, 1952, p. 404, from the lower part of the Mangazeya Formation (Chertovskian Horizon, *Nemagraptus gracilis* Biozone, lower Caradoc), Podkamennaya Tunguska River, southern Evenkia. Holotype, cranidium, PIN 589/169; figured Kramarenko (1952, fig. 1.9), Plate 3, figures 1, 4 herein.

Other species. *C. parnaica* Balashova, 1960a; *C. pentagona* Balashova, 1960a; *C. taimyrica* Balashova, 1960a; *C. viluensis* (Kramarenko, 1957).

Diagnosis. Glabella much narrower than cheek posteriorly, expanding very strongly forward between occipital furrow and transverse line through A3, thereafter with marked decrease in rate of expansion to

EXPLANATION OF PLATE 2

Except for 1–4, 6, 11 and 13, specimens are from the Mangazeya Formation (Caradoc), Evenkia; all photographs except 14–15 are of plaster replicas.

Figs 1–3. *Monorakos morkokensis* Maksimova, 1962; upper part of Dolbor Formation (lowermost Ashgill), Mas-Yurekh River, tributary of Morkoka River, Yakutia. 1, CNIGR 568/9202, glabella, paratype, dorsal view; $\times 2.75$. 2, CNIGR 570/9202, pygidium, holotype, dorsal view; $\times 3.25$. 3, CNIGR 569/9202, pygidium, paratype, dorsal view; $\times 2.5$.

Figs 4, 6. *Carinopyge?* *spinifera* Balashova, 1960a; Tolmachev Formation (Caradoc), upper reaches of Nizhnyaya Taimyra River, Taimyr Peninsula. CNIGR 104/8153, complete enrolled and compressed exoskeleton, holotype, dorsal view of pygidium and ventral view of hypostome, and dorsal view of cephalon and most of thorax; $\times 2$.

Figs 5, 9. *Monorakos ossacrum* Kramarenko, 1952; Podkamennaya Tunguska River. PIN 589/1000, cephalic doublure and hypostome, ventral view, and holotype cranidium, dorsal view, probably belonging to same individual; $\times 2$.

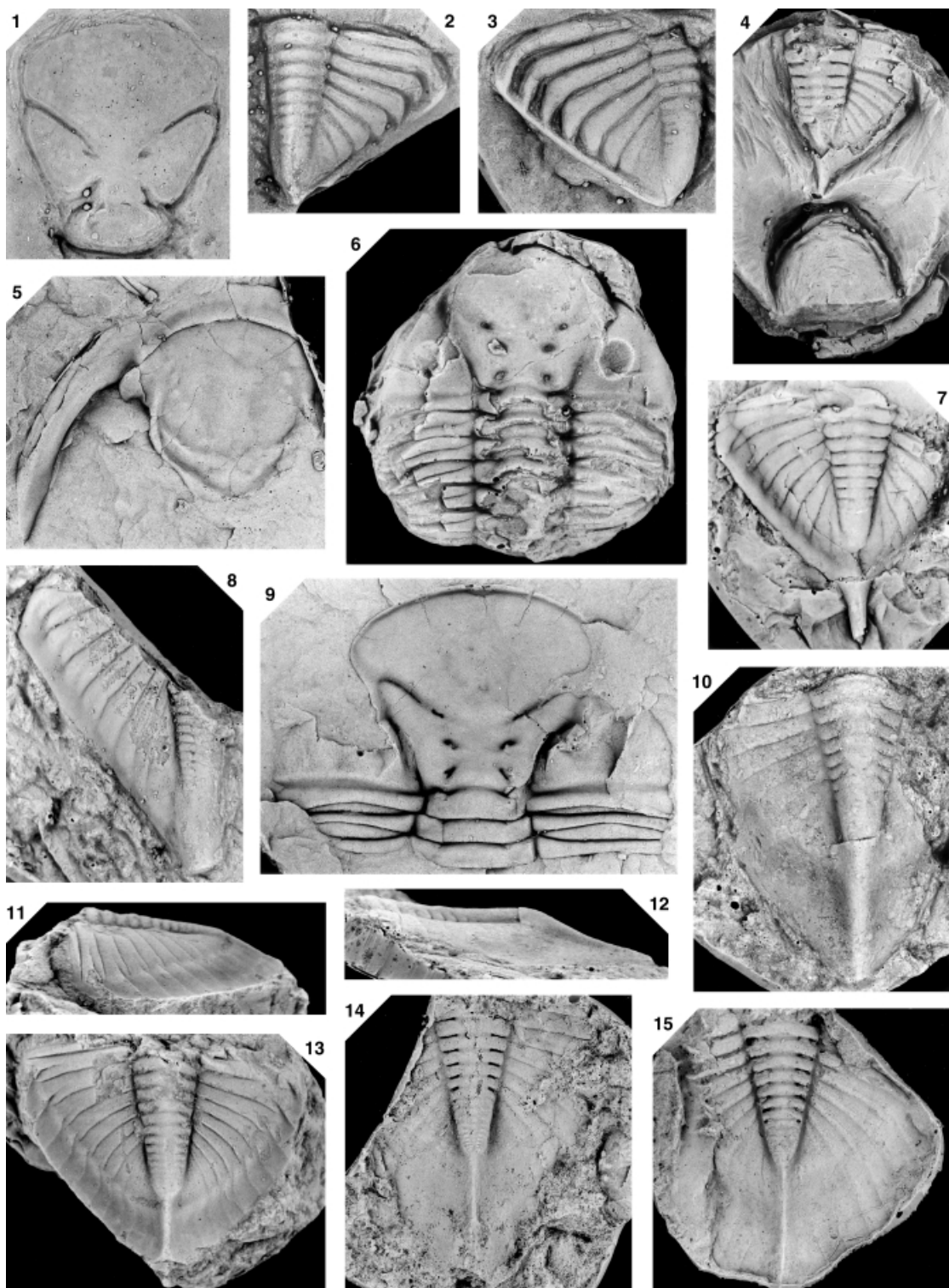
Fig. 7. *Carinopyge ensifera* Maksimova, 1955; Chunya River above confluence of Amutkan River. CNIGR 672/9202, pygidium, holotype, dorsal view; $\times 2.5$.

Fig. 8. *Carinopyge?* sp.; Podkamennaya Tunguska River. CNIGR 676/9202, incomplete pygidium, figured Maksimova (1962, pl. 16, fig. 4), dorsal view; $\times 2.5$.

Figs 10, 12, 14–15. *Carinopyge fracta* Maksimova, 1955. 10, 12, CNIGR 654/9202, pygidium, lectotype; Rybokupchaya River, tributary of Chunya River; dorsal and lateral views; $\times 1.75$. 14, CNIGR 655/9202, latex cast of external mould of pygidium, paralectotype; same locality as lectotype; dorsal view; $\times 1.75$. 15, CNIGR 653/9202, latex cast of external mould of pygidium, paralectotype; right bank of Chunya River; dorsal view; $\times 1$.

Figs 11, 13. *Carinopyge abscisa* Maksimova, 1955; lower part of Dolbor Formation (uppermost Caradoc–lowermost Ashgill), Podkamennaya Tunguska River, Evenkia. CNIGR 668/9202, pygidium, lectotype, lateral and dorsal views; $\times 2.5$.

PLATE 2



HOLLOWAY, *Carinopyge*, *Monorakos*

widest part of frontal lobe; width across frontal lobe more than twice width at occipital ring. Glabellar sculpture of fine to coarse tubercles, commonly of two sizes. Genal spine broad, flattened in cross section, bearing a deep longitudinal furrow. Pygidium subtriangular, without mucro; axis narrower than pleurae anteriorly; posterior pleural bands on anterior few segments elevated distally along their posterior edges and crossing border furrow to reach narrow, convex border.

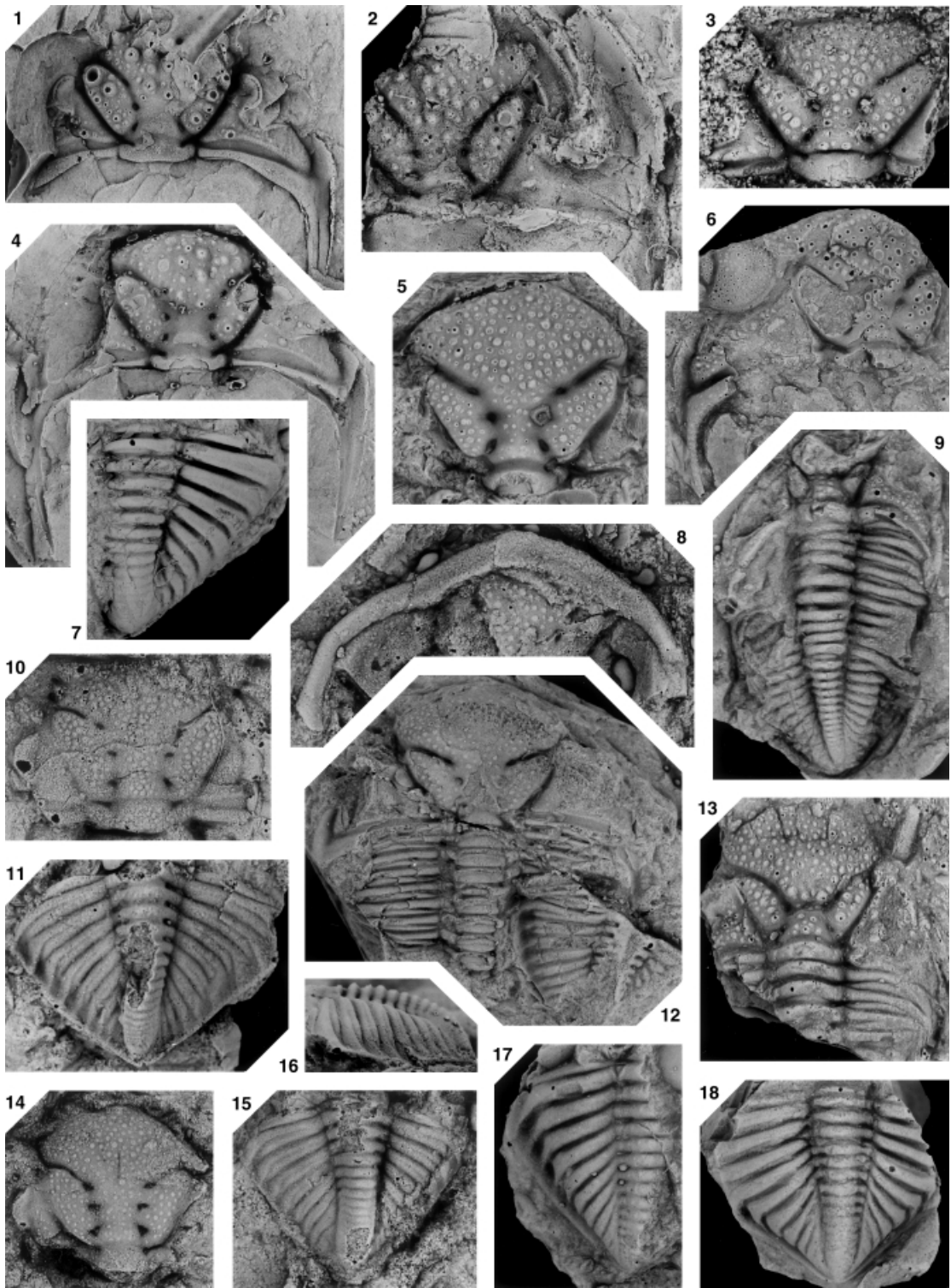
Remarks. According to Maksimova (1962, p. 128), the holotype of *C. armata* comes from the Mangazeya Formation, and Kanygin *et al.* (1988, p. 15) recorded the species from the lower part of the formation (Chertovskian Horizon). Two other cranidia of *armata* from the same horizon and region (Podkamennaya Tunguska River) were illustrated by Kanygin *et al.* (1977, pl. 6, figs 4–5). One of these cranidia was refigured by Semenova (1984, p. 81, pl. 28, fig. 8), who identified it as *C. taimyrica* Balashova, 1960a, and gave the stratigraphical horizon as the Dolbor Formation (uppermost Caradoc–lowermost Ashgill) in the text but as the Ust'stolbovaya Formation (upper Llanvirn) in the explanation to the plate. The identification as *taimyrica* is undoubtedly incorrect, as the specimen shows the very coarse glabellar tubercles characteristic of *armata* but absent in *taimyrica* (compare Pl. 3, figs 1, 4, 13). A cranidium from the Chertovskian Horizon of the Kuryeka River, Eastern Siberia, figured by Maksimova (1962, pl. 15, fig. 6) as *C. cf. armata*, differs from the holotype in the denser glabellar tuberculation of more uniform size, in these respects showing greater similarity to *C. pentagona* (see Pl. 3, figs 3, 5).

In cranidial morphology, *Ceratevenkaspis* is similar to *Monorakos* in that the glabella is narrower than the cheek posteriorly and expands strongly forwards, and the genal spine is broad, flattened in cross section and bears a deep longitudinal furrow. The cranidium of *Ceratevenkaspis* is distinguished from that of *Monorakos* by the even stronger expansion of the glabella between the occipital ring and the level of A3,

EXPLANATION OF PLATE 3

- Figs 1–2, 4. *Ceratevenkaspis armata* Kramarenko, 1952; lower part of Mangazeya Formation (Chertovskian Horizon, lower Caradoc), Podkamennaya Tunguska River, southern Evenkia. 1, 4, PIN 589/169, cranidium, holotype, latex cast of external mould, and internal mould, dorsal views; $\times 3.25$; circular pits in centre of tubercles are bubbles in casts. 2, PIN 589/613, cranidium, latex cast of external mould on same slab as paratype of *Parevenkaspis egloni* Kramarenko, 1952, dorsal view; $\times 4$.
- Fig. 3. *Ceratevenkaspis cf. pentagona* Balashova, 1960a; Chertovskian Horizon (lower Caradoc), Kuryeka River, Eastern Siberia. CNIGR 650/9202, cranidium; figured Maksimova (1962, pl. 15, fig. 6) as *Ceratevenkaspis cf. armata*; dorsal view; $\times 4.25$.
- Figs 5, 7. *Ceratevenkaspis pentagona* Balashova, 1960a; Tolmachev Formation (middle–upper Caradoc), upper reaches of Nyun'karaku-Tari River, eastern Taimyr Peninsula. 5, CNIGR 97/8153, cranidium, holotype, dorsal view; $\times 2.5$. 7, CNIGR 98/8153, pygidium, paratype, dorsal view; $\times 3$.
- Fig. 6. *Ceratevenkaspis parnaica* Balashova, 1960a; Povorotnaya River Formation (uppermost Caradoc–Ashgill), River Parnaya, right tributary of upper reaches of Nyun'karaku-Tari River, eastern Taimyr Peninsula. CNIGR 96/8153, cranidium, holotype, dorsal view; $\times 2$.
- Figs 8, 10–11, 14–16. *Ceratevenkaspis viluensis* (Kramarenko, 1957); unspecified stratigraphical horizon, basin of River Vilyuy, Yakutia. 8, PIN 589/1193, cephalic doublure, paratype, ventral view; $\times 4$. 10, PIN 589/1190, cranidium, paratype, dorsal view; $\times 4.5$. 11, PIN 589/1356, pygidium, paratype, dorsal view; $\times 3.75$. 14, PIN 589/1189, cranidium, holotype, dorsal view; $\times 3.25$. 15–16, PIN 589/1193, pygidium, paratype, on same slab as specimen in 8, lateral and dorsal views; $\times 4$.
- Figs 9, 13, 17–18. *Ceratevenkaspis taimyrica* Balashova, 1960a; Povorotnaya River Formation (uppermost Caradoc–Ashgill), lower reaches of Parnaya River, right tributary of upper reaches of Nyun'karaku-Tari River, eastern Taimyr Peninsula. 9, CNIGR 100/8153, dorsal exoskeleton, paratype, dorsal view; $\times 3$. 13, CNIGR 99/8153, cranidium and anterior part of thorax, holotype, dorsal view; $\times 3$. 17, CNIGR 101/8153, pygidium, paratype, dorsal view; $\times 3$. 18, CNIGR 102/8153, pygidium, paratype, dorsal view; $\times 3$.
- Fig. 12. *Ceratevenkaspis* sp.; Son Formation (lower Caradoc), Inanya River basin, south of Omulev Mountains, Magadan Region. PIN 4102/72, broken and partly disarticulated dorsal exoskeleton, figured Chugaeva (1964, pl. 6, fig. 12; 1968, pl. 42, fig. 5) as *Monorakos mutabilis* Kramarenko, 1952, dorsal view; $\times 3.5$.
- All photographs except 1–2 are of plaster replicas.

PLATE 3



HOLLOWAY, *Ceratevenkaspis*

the marked reduction in the rate of glabellar expansion in front of the level of A3, and the generally coarser glabellar tuberculation. On the basis of these characters, '*Monorakos*' *viluensis* Kramarenko, 1957, from the Vilyuy River, western Yakutia, is here assigned to *Ceratevenkaspis*. The pygidium of *C. armata* is unknown, and that of *C. parnaica* was not described or illustrated by Balashova (1960*a, b*), although she stated that she had one pygidium available to her. Pygidia of *C. taimyrica* (Pl. 3, figs 9, 17–18) and *C. viluensis* (Pl. 3, figs 11, 15–16) resemble those of *Monorakos* in the narrow axis and border, and the distally elevated posterior pleural bands crossing the border furrow. The pygidium assigned to *C. pentagona* (Pl. 3, fig. 7) lacks a border and the distally elevated posterior pleural bands, and may not be congeneric with the holotype cranidium (Pl. 3, fig. 5).

An incomplete dorsal exoskeleton with displaced pygidium, from the Inanya River basin, south of the Omulev Mountains in the Magadan Region of the Russian Far East, was identified by Chugaeva (1964, p. 55, pl. 6, fig. 12) as *Monorakos mutabilis* Kramarenko (see also Chugaeva 1968, p. 116, pl. 42, fig. 5). The specimen, which is from the Son Formation (lower Caradoc; see Orodovskaya 1988, p. 107), differs from the holotype of *mutabilis* in having a more strongly anteriorly expanding glabella with more obliquely oriented composite lobes, a more inflated frontal lobe, a deeper and more transversely directed S3, and a dense sculpture of fine tubercles on the glabella and at least the adaxial part of the fixigena (compare Pl. 1, fig. 8 with Pl. 3, fig. 12). The specimen is here assigned to *Ceratevenkaspis*, and it closely resembles *C. viluensis* in the shape and sculpture of the glabella as well as in pygidial morphology.

'*Ceratevenkaspis borealica* Balashova, 1960*a* (pl. 4, fig. 12*a–b*), from the Tolmachev Formation (Caradoc) of the Nizhnyaya Taimyra River, Taimyr Peninsula, is here excluded from the genus. The holotype and only illustrated specimen is a pygidium characterised by a distinctly funnel-shaped axis, with a posteriorly narrowing anterior half bearing well-developed apodemes, and a subparallel-sided posterior half without apodemes. Pygidial axial morphology of this type is characteristic of the Eomonorachinae, and it is likely that *borealica* belongs to a genus of that subfamily.

Stratigraphical range and distribution. Caradoc–Ashgill; Eastern Siberia (Evenkia, Taimyr), Russian Far East (Yakutia, Magadan Region).

EXPLANATION OF PLATE 4

Except for 11–13 and 15–17, specimens are from the Podkamennaya Tunguska River, southern Evenkia; all photographs except 4 are of plaster replicas.

Figs 1–5, 8. *Elasmaspis speciosa* Kramarenko, 1956; Dolbor Formation (uppermost Caradoc–lowermost Ashgill). 1–2, PIN 589/1264, cranidium, paratype, dorsal and oblique views; $\times 3.5$. 3, PIN 589/1267, cranidium, paratype, dorsal view; $\times 3.5$. 4, PIN 589/1263, cephalon, holotype, dorsal view; $\times 2.5$. 5, PIN 589/1266, cranidium, paratype, dorsal view; $\times 4.5$. 8, PIN 589/1265, cranidium, paratype, dorsal view; $\times 3.5$.

Figs 6, 9. *Evenkaspis (Evenkaspis) galeata* Kramarenko, 1958; Mangazeya (Maksimova 1962, p. 124) or Bur (Kanygin *et al.* 1988, p. 11) formations (Caradoc–Ashgill). PIN 589/1259, cephalon, holotype, oblique and dorsal views; $\times 2.75$.

Figs 7, 10. *Evenkaspis (Evenkaspis) axillaris* Kramarenko, 1958; uncertain stratigraphical horizon. PIN 589/1256, enrolled dorsal exoskeleton, holotype, dorsal view of cephalon, and lateral view; $\times 2.25$.

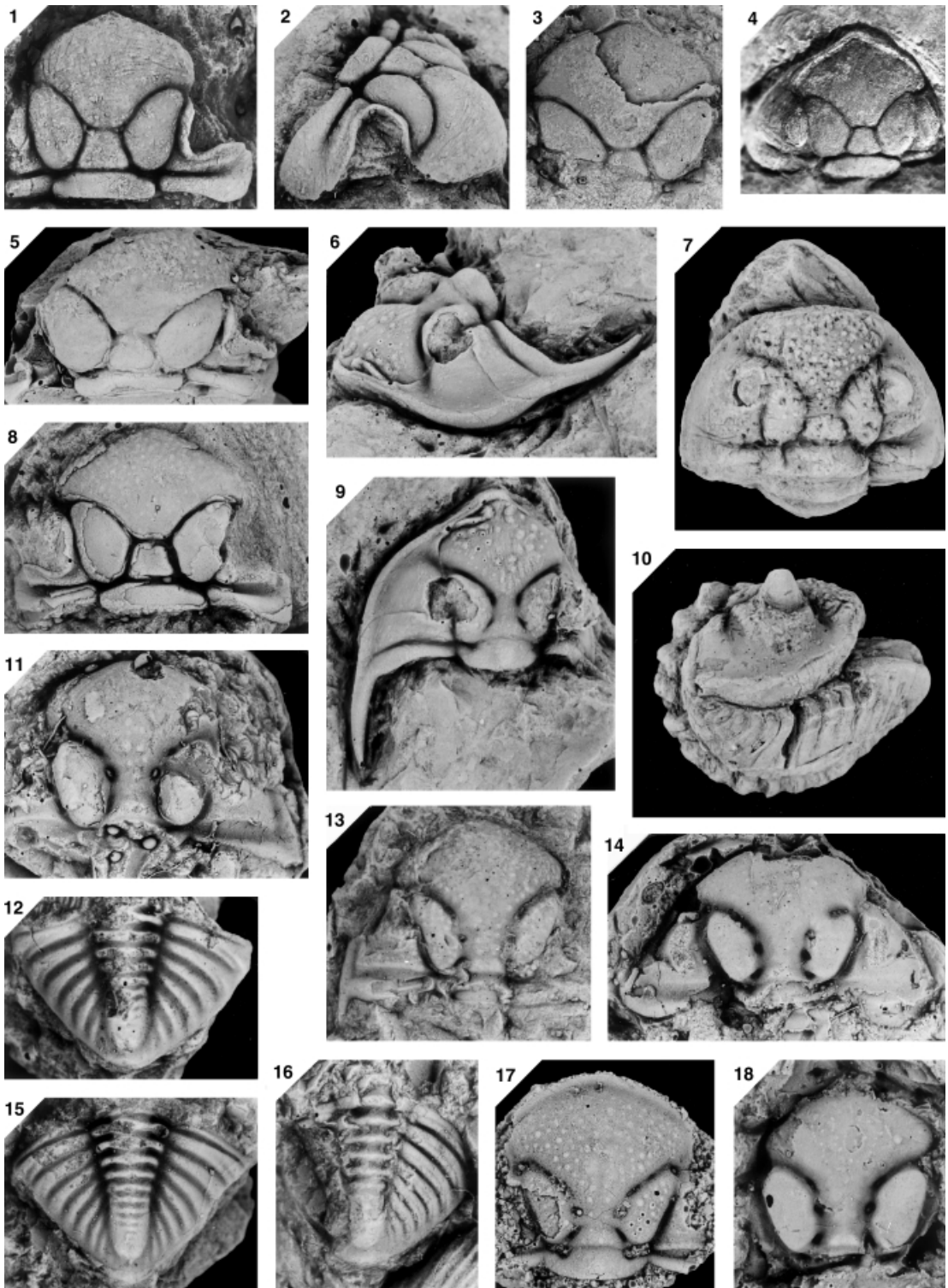
Figs 11–12, 15. *Evenkaspis (Evenkaspis) norilskiensis* Balashova, 1960*a*; Tolmachev or Povorotnaya River formations (Caradoc–Ashgill), upper reaches of Nyun'karaku-Tari River, eastern Taimyr Peninsula. 11, CNIGR 95/8153, cranidium, holotype, dorsal view; $\times 4.5$. 12, CNIGR 94/8153, pygidium, paratype, dorsal view; $\times 5$. 15, CNIGR 93/8153, pygidium, paratype, dorsal view; $\times 5$.

Figs 13, 16. *Evenkaspis (Evenkaspis) zlobini* (Balashova, 1960*a*); Tolmachev Formation (Caradoc), upper reaches of Klyuevka River, eastern Taimyr Peninsula. 13, CNIGR 91/8153, cranidium, holotype, dorsal view; $\times 3.75$. 16, CNIGR 92/8153, pygidium, paratype, dorsal view; $\times 5$.

Figs 14, 18. *Evenkaspis (Parevenkaspis) egloni* Kramarenko, 1952; Mangazeya Formation (lower Caradoc). 14, PIN 589/165, cephalon, holotype, dorsal view; $\times 4$. 18, PIN 589/613, glabella, paratype, dorsal view; $\times 3.75$.

Fig. 17. *Evenkaspis (Evenkaspis?)* aff. *galeata* Kramarenko, 1958; lower part of Mangazeya Formation (Chertovskian Horizon, lower Caradoc), Kuryeka River, southern Taimyria. CNIGR 621/9202, cranidium, figured Maksimova (1962, pl. 15, fig. 5), dorsal view; $\times 3.25$.

PLATE 4



HOLLOWAY, *Elasmaspis*, *Evenkaspis*

Genus ELASMASPIS Kramarenko, 1956

Plate 4, figures 1–5, 8

Type species. Original designation; *Elasmaspis speciosa* Kramarenko, 1956, p. 1031, from the Dolbor Formation (Dolborian Horizon, *Pleurograptus linearis* Biozone, uppermost Caradoc–lowermost Ashgill) of the Podkamennaya Tunguska River, southern Evenkia, Eastern Siberia. Holotype, cephalon, PIN 589/1263; figured Kramarenko (1956, fig. 1.1), Plate 4, figure 4 herein.

Other species. None named.

Diagnosis. Cephalon angular in outline anteromedially. Glabella wider than cheek posteriorly, abruptly increasing in width immediately in front of occipital ring, thereafter expanding forwards more gradually; width across frontal lobe *c.* 1.7 times width at occipital ring. Longitudinal furrow deep and narrow throughout, meeting occipital furrow posteriorly about half way between sagittal axis and distal end of occipital ring; longitudinal furrow joined across narrowest part of median lobe by deep, transverse furrow (S2). Minimum width of median lobe less than width of composite lobe measured across same transverse line. Palpebral lobe long (exsag.), extending from front of composite lobe almost to posterior border furrow, over most of its length rising directly from axial furrow; palpebral furrow present only posteriorly. Genal angle rounded.

Remarks. The type species is known only from a cephalon and several cranidia. These resemble *Evenkaspis* in the subangular anteromedial outline and the rather gently forwardly expanding glabella that is wider than the cheek posteriorly. However, *Elasmaspis* differs from *Evenkaspis* in having a sharply impressed, transverse furrow joining the longitudinal furrows across the median part of the glabella, and very narrow and deep longitudinal furrows in which apodemal pits are not apparent. *Elasmaspis* differs from *Evenkaspis* (*Evenkaspis*) additionally in having rounded rather than spinose genal angles.

The transverse furrow joining the longitudinal furrows in *Elasmaspis* is much shorter (sag.) and deeper than the shallow depression that in other monorakines commonly crosses the median part of L2. In *Elasmaspis* the transverse furrow is situated at the narrowest part of the median lobe, in line with the position where in other monorakines apodemal pit A2 is situated in the longitudinal furrow. Although the apodemal pits have not been observed in *Elasmaspis*, the position of the transverse furrow suggests that it is homologous with the median part of S2.

Kramarenko and Maksimova (1960, p. 171) stated that *Elasmaspis* is known from two species, but only the type species has been named. Semenova (1984, p. 81) recorded *E. speciosa* from the Dolbor Formation of the Podkamennaya Tunguska River (the type locality), and the upper part of the Dzherom Formation of the Moiero River farther to the north (see also Kanygin *et al.* 1988, p. 12). From the latter horizon and locality, Semenova (1984, pl. 50, fig. 5) illustrated an incomplete cranidium lacking most of the cheeks, but the specimen differs from the types of *speciosa* in having a longer (sag.) transverse furrow or depression crossing the median part of the glabella, and a correspondingly shorter (sag.) posteromedian lobe behind the transverse furrow or depression. These differences suggest that the transverse furrow or depression may be the depressed median part of L2 rather than S2, but this cannot be determined from the relationship of the depression to the apodemal pits, as these are not distinguishable in the longitudinal furrows. If the transverse depression is the depressed median part of L2, the cranidium may belong to *Evenkaspis* rather than to a new species of *Elasmaspis*.

Genus EVENKASPIS Kramarenko, 1952

Type species. Original designation; *Evenkaspis marina* Kramarenko, 1952, p. 404 [= *Phacops (Monorakos) sibiricus* Schmidt, 1886, p. 507], from the Mangazeya Formation (Caradoc) of the Podkamennaya Tunguska River, southern Evenkia. Holotype of *marina*, cranidium PIN 589/13; figured Kramarenko (1952, fig. 1.6), Plate 5, figure 1 herein.

Diagnosis. Cephalon subangular in outline anteromedially; glabella as wide as or wider than cheek posteriorly, expanding gently to moderately forwards, width across frontal lobe 1.25–1.7 times width at occipital ring; glabellar sculpture of tubercles. Lateral cephalic border convex (tr.), steeply inclined.

Remarks. The type species of the genus is *Evenkaspis marina*, not *Phacops (Monorakos) sibiricus* Schmidt, 1886 as stated by Kramarenko and Maksimova (1960, p. 169), Maksimova (1962, p. 117) and Ormiston (1978, p. 345). However, Maksimova (1962) considered *marina* to be a junior synonym of *sibiricus*, which was described from the same region as the former on the basis of ‘... a glabella and an impression of the same’ (Schmidt 1886, p. 507; my translation). It is not clear from the original text whether Schmidt meant that the impression was the external mould of the first specimen or of a different one; however, I conclude that he was referring to two specimens, as the slab of rock labelled as the type in the collections of the Palaeontological Institute, Moscow (PIN 228/224) includes an internal mould of a small cranidium (Pl. 5, fig. 2) and an external mould of a larger one (Pl. 5, fig. 4). Also present on the slab are internal moulds of several pygidia that Schmidt apparently did not recognize as belonging to the same species as the cranidia. The smaller cranidium, which corresponds in size and completeness with Schmidt’s (1886, pl. 30, fig. 10) illustration, is here designated lectotype. This designation is made in order to confirm the identity of the species (ICZN Article 74.7.3). Comparison of the types of *sibiricus* with the holotype of *marina* demonstrates their similarity and supports Maksimova’s (1962) conclusion on the synonymy of the two species.

Evenkaspis is here considered to include the subgenera *E. (Evenkaspis)*, in which a genal spine is present, and *E. (Parevenkaspis)*, which lacks a genal spine. As the pygidium of *E. (Parevenkaspis)* is unknown, the diagnosis of *Evenkaspis* includes only cranidial characters. Morphological comparisons between *Evenkaspis* and *Monorakos* are made below with the nominotypical subgenus of the former.

Subgenus EVENKASPIS (EVENKASPIS) Kramarenko, 1952

Plate 4, figures 6–7, 9–13, 15–17; Plate 5, figures 1–19

Type species. As for genus.

Other species. *E. (E.) axillaris* Kramarenko, 1958; *E. (E.) galeata* Kramarenko, 1958; *E. (E.) ivanovae* Kramarenko, 1952; *E. (E.) lobata* Kramarenko, 1958; *E. (E.) nikiforovae* Maksimova, 1962; *E. (E.) nordica* (Balashova, 1960a); *E. (E.) norilskiensis* Balashova, 1960a; *E. (E.) sibirica* (Schmidt, 1886); *E. (E.) zlobini* (Balashova, 1960a); *E. (E.?) schmidti* (Toll, 1889); *E. (E.?) tchunensis* Maksimova, 1962.

Diagnosis. *Evenkaspis* with slender genal spine that is rounded in cross section but may bear shallow longitudinal furrow at its base. Pleural tips on posterior thoracic segments not deflected backwards. Pygidium subparabolic in outline; axis as wide or wider than pleurae anteriorly, commonly poorly differentiated from steeply inclined and slightly backwardly projecting postaxial region; axial furrow shallow; pleurae strongly convex (tr.), without concave border.

Remarks. Struve (1959) regarded *Evenkaspis* as a subgenus of *Monorakos*, but I consider *Evenkaspis (s.s.)* to be more closely related to *Parevenkaspis* and *Elasmaspis* (see discussion of evolutionary relationships below). *E. (Evenkaspis)* differs from *Monorakos* in the glabella that is wider posteriorly in relation to the cheek but expands more weakly forwards; the rounded and steeply inclined rather than flattened lateral cephalic border (compare Pl. 5, figs 16, 18 with Ormiston 1978, pl. 1, figs 4–5); the genal spine that is slender and rounded in cross section, rather than broad and flattened with a strong longitudinal furrow extending most of its length (compare Pl. 4, figs 6, 9 with Ormiston 1978, pl. 1, fig. 2); the subparabolic rather than subtriangular pygidium; the narrower pygidial pleurae lacking a concave border; and the posterior pleural bands that are not distinctly raised distally. Comparison of the diagnoses for *Monorakos* and *Evenkaspis* given by Struve (1959), and Kramarenko and Maksimova (1960) (see also Maksimova 1962, table on p. 107), indicates that those authors considered *Evenkaspis* to be distinguished also by the more convex glabella and/or the more inflated composite lobes, but undeformed specimens of *Monorakos* appear to show little difference from most *Evenkaspis* species in these respects.

Based on the characters listed above, Balashova’s (1960a, b) species ‘*Monorakos nordicus* (Pl. 5, figs 3, 7) and ‘*M. zlobini* (Pl. 4, figs 13, 16) from the eastern Taimyr Peninsula are here placed in *E. (Evenkaspis)*. I agree with Kramarenko (1957, p. 50) and Maksimova (1962, p. 118) that ‘*M. schmidti* Toll (1889, pl. 3,

fig. 2), from Kotelny Island in the New Siberian Islands, belongs to *Evenkaspis*, based on the weakly forwardly expanding glabella of the single known, incomplete cranidium; this species is here tentatively assigned to *E. (Evenkaspis)* because it is not known whether genal spines are present.

Stratigraphical range and distribution. Caradoc–Ashgill; Eastern Siberia (Evenkia, Eastern Taimyr), Russian Far East (New Siberian Islands).

Subgenus EVENKASPIS (PAREVENKASPIS) Kramarenko, 1952

Plate 4, figures 14, 18

Type species. Monotypy; *Parevenkaspis egloni* Kramarenko, 1952, p.404, from the lower part of the Mangazeya Formation (Chertovskian Horizon, *Nemagraptus gracilis* Biozone, lower Caradoc), Podkamennaya Tunguska River, southern Evenkia, Eastern Siberia. Holotype, cephalon, PIN 589/165; figured Kramarenko (1952, fig. 1.8)

Other species. None known.

Diagnosis. *Evenkaspis* with genal angle strongly rounded, lacking spine.

Remarks. The type species is known only from the holotype cephalon and an incomplete cranidium consisting mainly of the glabella in front of the occipital ring; both specimens are rather poorly preserved internal moulds. The stratigraphical horizon of the specimens has not previously been reported, but they are accompanied on the same pieces of rock by cranidia of *E. (Evenkaspis) sibirica* and *Ceratevenkaspis armata*, the type specimens of which are from the lower part of the Mangazeya Formation. The diagnosis of *Parevenkaspis* given by Kramarenko (1952) and Kramarenko and Maksimova (1960) states that the glabella expands strongly forwards and the eyes are highly elevated (see also Maksimova 1962, table on p.107). However, the glabella does not expand more strongly forwards than in some species of *E. (Evenkaspis)* (e.g. compare Pl. 4, fig. 14 with Pl. 5, fig. 16), and is not as strongly expanded as in *Monorakos*. The glabella is approximately as wide posteriorly as the cheeks, in this respect also

EXPLANATION OF PLATE 5

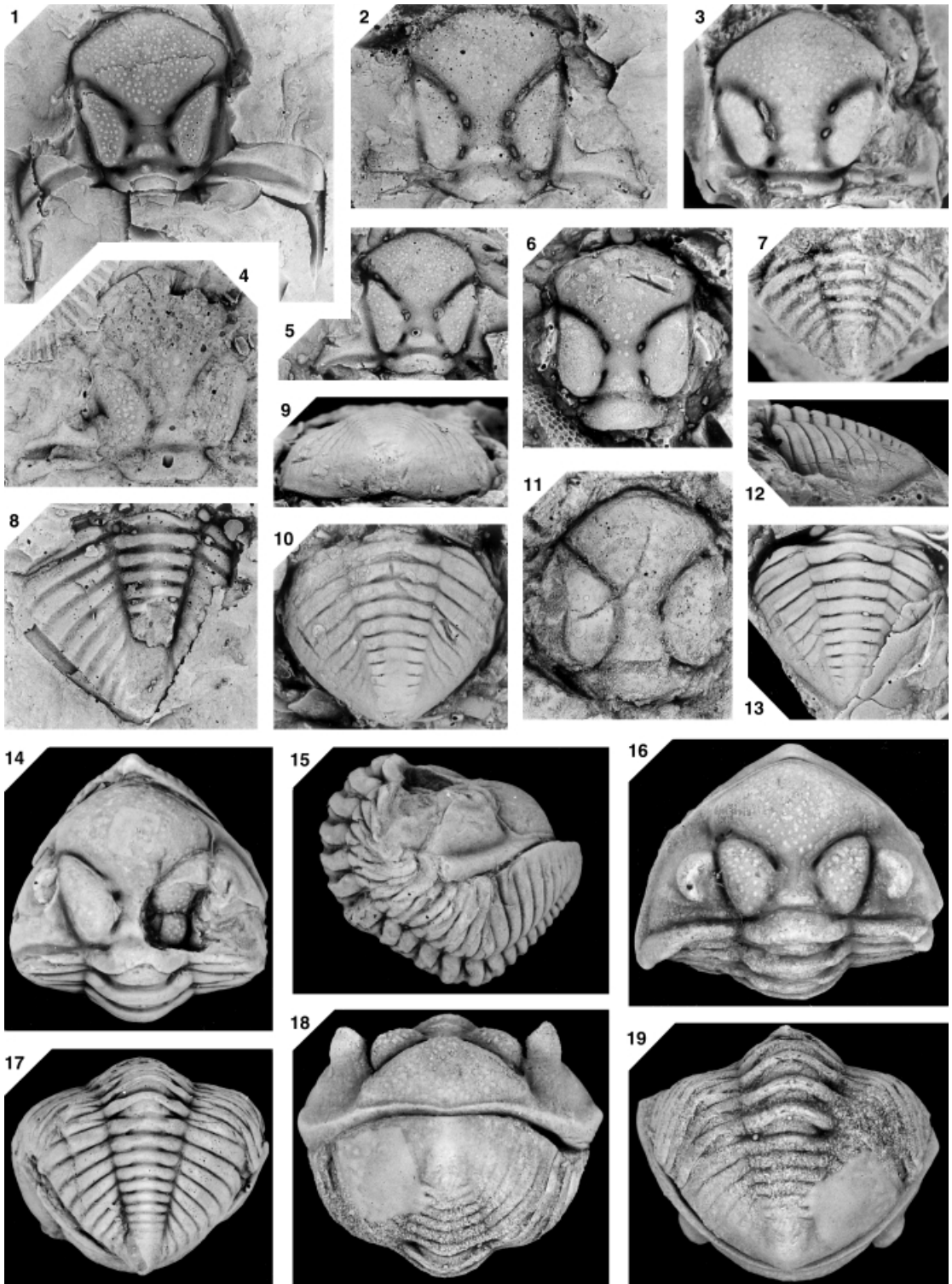
Unless stated otherwise, specimens are from the Mangazeya Formation (Caradoc) of the Podkamennaya Tunguska River, southern Evenkia; all photographs except 4 are of plaster replicas.

Figs 1–2, 4–5, 8, 14–15, 17. *Evenkaspis (Evenkaspis) sibirica* (Schmidt, 1886). 1, PIN 589/13, cranidium, holotype of *Evenkaspis (Evenkaspis) marina* Kramarenko, 1952, dorsal view; ×2. 2, PIN 228/224, cranidium, lectotype, dorsal view; ×3. 4, PIN 228/224, cranidium, paralectotype, latex cast of external mould, dorsal view; ×2. 5, PIN 589/1357, small cranidium on same slab as paratype of *Monorakos planus* Kramarenko, 1957, dorsal view; ×4. 8, PIN 228/224, pygidium on same slab as lectotype and paralectotype cranidia, dorsal view; ×3. 14–15, 17, CNIGR 594/9202, enrolled dorsal exoskeleton, figured Maksimova (1955, pl. 31, fig. 1a–d, as *Evenkaspis marina* Kramarenko, 1952; 1962, pl. 15, fig. 1a–d), dorsal view of cephalon, lateral view, and dorsal view of pygidium; ×1.5.

Figs 3, 7. *Evenkaspis (Evenkaspis) nordica* (Balashova, 1960a); Tolmachev Formation (Caradoc), Klyuch Parallel'nyi, right tributary of upper reaches of Nyun'karaku-Tari River, eastern Taimyr. 3, CNIGR 89/8153, cranidium, holotype, dorsal view; ×3.75. 7, CNIGR 90/8153, pygidium, dorsal view; ×7.

Figs 6, 9–13. *Evenkaspis (Evenkaspis?) tchunensis* Maksimova, 1962. 6, CNIGR 635/9202, cranidium; Chunya River; dorsal view; ×5. 9–10, CNIGR 637/9202, pygidium, holotype; Chunya River; posterior and dorsal views; ×3. 11, CNIGR 636/9202, cranidium; Rybokupchaya River, tributary of Chunya River; dorsal view; ×3.25. 12–13, CNIGR 637/9202, pygidium on same slab as holotype pygidium; Chunya River; lateral and dorsal views; ×3.

Figs 16, 18–19. *Evenkaspis (Evenkaspis) nikiforovae* Maksimova, 1962; Mangazeya Formation, Baksanian Horizon (Maksimova 1962, p.206) or lower part of Dolbor Formation (Kanygin *et al.* 1988, p.11) (Caradoc–lowermost Ashgill). CNIGR 614/9202, enrolled dorsal exoskeleton, holotype, figured Maksimova [1955, pl. 30, fig. 1a–d, as *Evenkaspis sibiricus (sic)*; 1962, pl. 15, fig. 9a–d], dorsal view of cephalon, anterior view of enrolled exoskeleton, and dorsal view of pygidium; ×3.



HOLLOWAY, *Evenkaspis*

resembling *E. (Evenkaspis)* rather than *Monorakos*. The eyes are broken off in the holotype of *P. egloni*, but there is no distinguishable difference from other monorakines in their height on the cheeks. The only observable difference from *E. (Evenkaspis)* is the absence of genal spines, and in all but this feature the cranial morphology of *E. (P.) egloni* is so similar to that of species such as *E. (E.) norilskiensis* (Pl. 4, fig. 11), *E. (E.) nordica* (Pl. 5, fig. 3) and *E. (E.) zlobini* (Pl. 4, fig. 13), that it may be questioned whether *E. (Parevenkaspis)* deserves recognition as a separate subgenus. The resolution of this question must await the availability of more complete material of *egloni*, including pygidia.

EVOLUTIONARY RELATIONSHIPS

The Monorakinae probably had its evolutionary origins in the Pterygometopinae, and Whittington (1966, p. 726) and Ludvigsen and Chatterton (1982, p. 2180) suggested a derivation from *Pterygometopus*. However, *Monorakos* has more in common morphologically with *Achatella* than with *Pterygometopus*, in features such as the glabella that is narrowest posteriorly (instead of across L2 as in *Pterygometopus*), the markedly oblique S3 and correspondingly long (sag.) frontal lobe, the shallow preglabellar furrow, the long, flattened and longitudinally furrowed genal spines, and the subtriangular, multi-segmented pygidium with a distinct border furrow. The appearance of *Achatella* in the upper Llanvirn (Uhaku Stage of Estonia; Jaanusson and Ramsköld 1993, p. 766) predates that of *Monorakos* in the Caradoc, so that *Monorakos* may have been derived from *Achatella* or the two genera may share a common ancestor. However, the two genera have different palaeogeographical distributions, *Monorakos* in Siberia and Arctida, and *Achatella* in Baltica and (by the middle Caradoc; Ludvigsen and Chatterton 1982, p. 2180) Laurentia.

Monorakos, *Carinopyge* and *Ceratevenkaspis* share a number of characters, including the glabella that is narrower (tr.) than the cheek posteriorly and expands strongly forward; the broad, flattened, and longitudinally furrowed genal spine (not known with certainty in *Carinopyge*); the pygidial axis that is narrower than the pleurae anteriorly; the well-defined pygidial border; and the distally elevated posterior pleural bands on the pygidium. These characters are reminiscent of *Achatella* and are regarded as primitive for the Monorakinae. Corresponding characters of *Evenkaspis (Evenkaspis)* regarded as derived are the gently forwardly expanding glabella that is as wide as or wider than the cheeks posteriorly; the slender genal spine that is rounded in cross section; the pygidial axis that is as wide as or wider than the pleurae anteriorly; and the absence of a border and of distally elevated posterior pleural bands on the pygidium. The similarity of *Evenkaspis (Parevenkaspis)* and *Elasmaspis (Evenkaspis)* in the shape of the glabella suggests that these three taxa share a common ancestry.

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