

# OLENELLACEAN TRILOBITES FROM EASTERN NORTH GREENLAND

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*Olenellus* cf. *svalbardensis* from the fold belt in eastern North Greenland and *Holmia hyperborea* n. sp. from the foreland region in Peary Land are described. *Holmia hyperborea* n. sp. is compared statistically with *Holmia kjerulfi*, *Olenellus gilberti*, and *Olenellus clarki*. Some aspects of the ontogenetic development of *Holmia hyperborea* n. sp. are discussed.

В работе описаны трилобиты *Olenellus* cf. *svalbardensis*, Встреченный в складчатом поясе восточной части северной Гренландии, и *Holmia hyperborea* n.sp. из предгорной области Пирилэнд. Дается статистическое сопоставление *Holmia hyperborea* n.sp. с *Holmia kjerulfi*, *Olenellus gilberti* и *Olenellus clarki*. Рассматриваются некоторые стороны онтогенетического развития *Holmia hyperborea* n.sp.

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Most geological field work up to now in northern Greenland has had the character of reconnaissance mapping and incidental collection of conspicuous fossiliferous samples. This is due to the short field season in a region which is only accessible with extreme difficulty and at high costs. Previous work and results are excellently summarised by Dawes (1971).

The Lower Cambrian olenellacean material described and discussed here belongs to two collections from different localities. In 1949 J. C. Troelsen collected a few samples from a hard fine-grained shale at G. B. Schley Fjord (map, fig. 1) in northern Peary Land within the North Greenland fold belt (see Troelsen, 1956). His material is here described for the first time. The other collection, made by geologists of Greenarctic Consortium in 1969 and presented to the Geological Survey of Greenland by J. Stuart Smith (J. C. Sproule and Associates Ltd., Calgary), was obtained from Børglum Elv, north of Jørgen Brønlund Fjord (map, fig. 1) during a reconnaissance survey. This material is contained in a dark fine-grained, highly fissile shale from the foreland facies south of the fold belt.

Indeterminable olenellacean fragments had previously been secured by Jepsen in 1968 from the Buen Formation at roughly the same stratigraphical

level further to the west, north of Jørgen Brønlund Fjord (Jepsen, 1971), and Troelsen (1950, 1956) recorded olenellid fragments associated with *Salterella* sp. from thin phosphoritic laminae at the base of the Brønlund Fjord Dolomite. The trilobites in this material, containing *Bonnia* and olenellids, will be described by the author in a coming paper. Further data on Lower Palaeozoic and younger samples collected in eastern North Greenland by J. C. Troelsen and E. Knuth 1947–1950 may be found in Peel, Dawes & Troelsen (1974).

Additional beds of supposed Lower Cambrian age in eastern North Greenland include the Kap Holbæk Sandstone and the overlying Danmark Fjord dolomite in the inner part of Danmark Fjord about 200 km to the southeast of Peary Land – here within the foreland regime of the Caledonian geosyncline in East Greenland. No fossils have been found, apart from *Skolithos*-like tubes in the Kap Holbæk Sandstone, and the Lower Cambrian age is inferred from the lithological agreement with the sections in the Jørgen Brønlund Fjord (Cowie, 1961, p. 29).

However, an almost cyclic repetition of arenaceous to dolomitic beds makes correlations on lithological grounds unsafe until further information

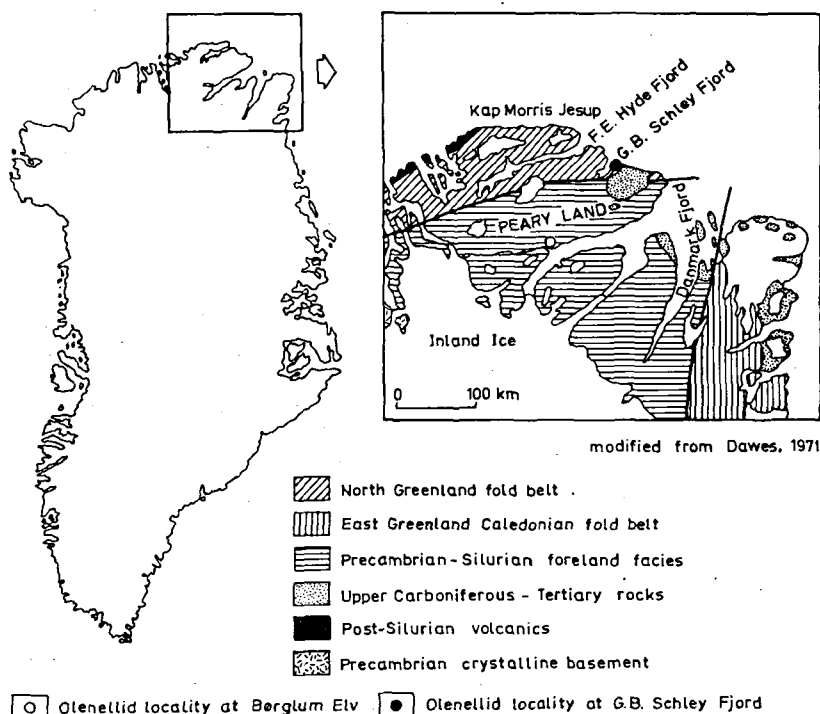


Fig. 1. Geological sketch-map of eastern North Greenland showing the two localities with olenellacean trilobites. Data from Dawes, 1971.

has been obtained with regard to lateral variations in facies and relations to the structural regimes. Dawes (1971, p. 226) correlated the Schley Fjord Shale with the Buen Formation in southern Peary Land, but the section at G. B. Schley Fjord does not contain an equivalent to the Brønlund Fjord Dolomite, as the shale is overlain by the Ordovician Wandel Valley Limestone following a simple erosional disconformity, and the olenellaceans in the two areas belong to different genera. So conclusions must be limited to the general statement of a Lower Cambrian age.

A single sample of a bituminous limestone from northern Nyeboe Land (central North Greenland) has revealed another occurrence of Lower Cambrian faunas. The sample contains indeterminate olenellacean fragments (Peel, 1974).

The material described and figured here is in the collections of the Mineralogical and Geological Museum of the University of Copenhagen, filed as MMH nos. 13005–13025.

Jan Aagaard has done the photographic work, and Miss A. Demin made the translation into Russian of the abstract.

### Olenellacean trilobites from G. B. Schley Fjord

Troelsen (1956) described the Schley Fjord Shale, which is probably less than 100 m thick, from the entrance to the fjord, see map in fig. 1. The boundary to the overlying Ordovician Wandel Valley Limestone is a simple erosional disconformity, while the contact to the underlying shale (Eocambrian?) has not been observed. The olenellaceans in the Schley Fjord Shale establish a Lower Cambrian age. Cowie (1971, p. 368) correlated the Schley Fjord Shale with the dolomites of the Danmark Fjord and Brønlund Fjord Formations, but correlations between sequences with different lithology from the fold belt and the foreland region should be avoided until a correspondence in faunal content at the species level can be demonstrated. Dawes (1971, p. 226) correlated the Schley Fjord Shale with the Buen Formation in southern Peary Land on the grounds that both formations had yielded an olenellacean fauna, but *Holmia*, which is the sole genus known from the Buen Formation, has not been found at G. B. Schley Fjord. Again, closer correlation should be avoided until more material is available.

The material collected by Troelsen in 1949 on a small island on the south side of the entrance to the fjord is contained in a medium-grey hard shale or slate with a slightly irregular cleavage. There is no indication of which level or levels the samples originate from. The olenellacean specimens, which are only represented by fragments, are all collected from weathered surfaces, and the resulting imperfect state of preservation does not permit a definite assignment to species. Only *Olenellus* appears to be represented.

Genus *Olenellus* Billings, 1861

The *Olenellus-Paedeumias* group has been debated for quite a few years, and Cowie (1968, pp. 13–16) summarizing the discussion of the relationships between the two genera concluded that *Paedeumias* is valid if several listed cephalic features are present, inter alia a narrow cephalic border. *Paedeumias* was retained as a valid genus by Palmer (1957) who was able to demonstrate significant differences throughout the ontogenetic development of *Olenellus* and *Paedeumias*, and he considered the consistently narrower cephalic border in the latter to be a character of generic value. Apparently *Paedeumias* was based on a young *Olenellus*, and it has been suggested that *Paedeumias* should be suppressed as a younger synonym of *Olenellus*, a view most recently expressed by Fritz (1972, pp. 11–12). Finally, Palmer (1973, oral communication) has obtained additional olenellid material which shows that the cephalic border width only has significance at the species level. All the available evidence thus suggests suppression of the generic name *Paedeumias* and in the present paper the species *clarki* is assigned to *Olenellus*.

*Olenellus* cf. *svalbardensis* Kielan, 1960

Pl. 1, figs. 1–3

Material. – One incomplete exoskeleton with more than half of the cephalon missing, five incomplete cephalae, one incomplete extraocular gena. All the specimens are preserved as weathered internal or external moulds.

Description. – The outline of the cephalon is approximately semicircular with its greatest width slightly in front of posterior border. Cephalic border with low relief is relatively narrow in front of glabella, widening in posterior direction to a maximum width in the vicinity of the long, slightly arcuate genal spines; posterior border is narrower than lateral border, curving gently outward-forwards to the slightly advanced genal spines. Intergenal spines are not preserved in any of the specimens. Border furrow is moderately wide and shallow throughout. Glabella is slightly expanded forward, leaving a distinct preglabellar field in front. Frontal glabellar lobe is large, evenly rounded anteriorly. The lateral glabellar furrows are not preserved in any of the cephalae. Occipital furrow is deeply impressed laterally, shallowing up mesially; occipital ring is simple, provided with a small mesial node. The dorsal furrow is moderately impressed. The palpebro-ocular ridge (Bergström, 1973) is strongly arched, divided by a shallow longitudinal furrow into anterior and posterior branches which join the frontal glabellar lobe at a level slightly behind midpoint of lobe; the palpebral furrow is deeply im-

pressed, Genae are moderately convex, the part inside the palpebral furrow is situated at a higher level than the extraocular parts of genae. A fairly coarse genal prosopon is seen as radiating, anastomosing ridges with small nodes at points of furcation; the markings stop at the border furrow.

Thorax probably contains about fifteen segments (posterior part of thorax not preserved). The thorax is conspicuously narrower than cephalon, gradually tapering in posterior direction. The third segment appears to be macropleural, but not very strongly so. The first two segments have an almost transverse orientation, whereas segments posterior to the macropleura are more strongly deflected. The axial ring is of common olenellid type, no axial spines are preserved. Pleural furrows are fairly deep and continue into the deflected part of the pleurae which are projected into moderately long, gently curved spines, directed obliquely backwards. Posterior part of thorax and pygidium are not preserved.

Dimensions. – Approximate dimensions of the incomplete exoskeleton shown in pl. 1, fig. 1: Length of carapace = 30 mm. Maximum width of carapace (excluding genal spines) = 24 mm. Length of cephalon = 12 mm. Width of cephalon (in front of genal spines) = 24 mm. Length of thorax = 18 mm. Maximum width of thorax = 16 mm.

Remarks. – All preserved features, including the morphology of the genal prosopon perfectly match the description of *Olenellus svalbardensis* Kielan, 1960 from Spitsbergen. The author definitely believes that the Peary Land material is conspecific with the Spitsbergen form, but an ultimate decision must wait until the morphology is known in fine detail. A free exchange of species between the two regions is only to be expected, when the proximity of Spitsbergen to eastern North Greenland, before the opening of the present North Atlantic, is taken into consideration.

Thus, the Schley Fjord Formation may probably be correlated with the Sofiekammen Formation in the Hekla Hoek Succession of Hornsund, Spitsbergen.

### Olenellacean trilobites from Børglum Elv

Most of the trilobite specimens, which are preserved in a highly fissile dark shale, are slightly distorted or broken due to flattening. Apart from differences related to different growth stages the olenellacean material appears to be rather homogeneous and may be assigned to a single new species of *Holmia*.

*Holmia hyperborea* n. sp.

Pl. 1, figs. 4–7; pl. 2, figs. 1–6; pl. 3, figs. 1–8

Derivation of name. – Latin *hyperborea* (us) = very far north.

Holotype. – Ventrally exposed small, almost complete dorsal exoskeleton belonging to an early holaspid stage (MMH no. 13008; from GGU collection 100824), pl. 1, fig. 4. Measurements of the holotype are listed in table 1, p. 90.

Other material. – 16 isolated, more or less complete holaspid cephalata and 4 meraspid cephalata, and 4 larger thoracic fragments with contiguous segments and parts of cephalon. All specimens are from GGU collection 100824.

Horizon and locality. – Upper part of the Buen Formation in a section above Brillesø, about 1.5 km east of Børglum Elv, Peary Land (map, fig. 1).

Diagnosis. – Cephalon of common holmiid type with well-advanced genal spines and intergenal spines in a fairly proximal position. Cephalic border narrower than usual for the genus. Thorax with 16 segments terminating in long pleural spines directed obliquely backwards.

Description. – Cephalon rounded inverted-trapezoidal in outline with its greatest width at a transverse line passing through the palpebral midpoints. Cephalic border is flat, delimited by a shallow and narrow border furrow, although details of the border morphology may be obscured by flattening; it is widest in the vicinity of the genal spine. The slender, moderately long genal spines, which are directed obliquely backwards, have their bases situated opposite the palpebral midpoints. Cephalic border behind the advanced genal spines is straight or curves gently backwards to the proximally situated intergenal spines which delimit the short, transverse part of posterior border. The somewhat clavate glabella reaches anterior border furrow in some adult specimens, whereas a narrow preglabellar field is found in meraspides and some holaspides, in the latter produced in a few instances by flattening(?) subsequent to decalcification of the exoskeletons. Frontal glabellar lobe broadly rounded anteriorly, only slightly expanded; it is somewhat crushed in all specimens and must originally have been bulbous, raised above the posterior part of glabella. The slightly oblique lateral glabellar furrows and occipital furrow are deeply impressed close to the dorsal furrow,

only the occipital furrow and anterior pair of glabellar furrows (S3) cross the glabella, shallowing up mesially. The occipital ring, which carries a short mesial spine, is slightly wider than the preceding part of the rhachis, but otherwise shows a perfect serial similarity (Bergström, 1973). The dorsal furrow is well-defined, deeply impressed behind the palpebro-ocular ridges (Bergström, 1973) which are long and wide, evenly curved. The palpebro-ocular ridge is divided into an anterior ridge which joins the frontal glabellar lobe at a level slightly behind the midpoint of the lobe, and a posterior ridge which smoothly merges with the posterior part of frontal glabellar lobe. Posteriorly the palpebro-ocular ridge touches another distinct ridge which runs inward-forwards from the intergenal spine across posterior border and fades out at a short distance from posterior part of the preoccipital glabellar lobe. Genae show only a moderate relief, but must originally have been more strongly convex. A genal prosopon consisting of radiating faint ridges in an anastomosing pattern with superimposed indistinct granules is seen in all specimens, and short discontinuous raised lines parallel to the margin are seen on the cephalic border. The hypostome is unknown.

The thorax, which consists of 16 segments with great serial similarity, is considerably narrower anteriorly than cephalon, attaining its greatest width at the fifth segment, tapering evenly therefrom in posterior direction. The pygidium, which is only known in outline, is minute, rounded rectangular. The axial rings are moderately long and wide, most of them carrying a short mesial spine, whereas one or several of the posterior tergites carry a long spine, as suggested by impressions of spines behind the pygidium in the ventrally exposed exoskeletons. The crescentic articulation half-ring is short (sag.) and delimited from the axial ring by a deeply impressed transverse furrow which is narrow distally, expanded mesially, thereby reducing the mesial length (sag.) of the axial ring. No other forms of articulation devices are preserved in the available specimens. The dorsal furrow is narrow, but apparently well-impressed. The straight, transverse part of the pleura is short (tr.), as the distal part abruptly turns obliquely backwards and is projected into a long and slender, gently curved spine. A wide and deeply impressed pleural furrow divides the pleura into an anterior and posterior pleural band of roughly equal dimensions, becoming more shallow and effaced distal to the deflection, so that the pleura gradually merges with the spine. One specimen (pl. 3, fig. 1) is bent sideways, the posterior part of thorax forming an angle of about  $50^\circ$  to a sagittal axis through cephalon and anterior part of thorax; in this position the pleural spines on the concave side come together in a smooth, slender bundle, and thus a considerable flexibility is evident.

The material contains some poorly preserved meraspid cephalata (pl. 3, figs. 5–8). The meraspid cephalon is subrectangular in outline with a nar-

row, almost transverse anterior border which is bounded anterolaterally by short procranial spines. The lateral border is almost parallel to sagittal axis and continues straight backwards into an advanced, relatively short genal spine. Border furrow is deeply impressed throughout, except at the intergenal spine, which is about twice the cephalic length and thus much more prominent than the genal spine. The intergenal spine continues adaxially into an expanding ridge which transgresses posterior border and border furrow and terminates as an apparently unsegmented pyriform bulb opposite the preoccipital lobe and L2. No traces of genal segmentation are preserved. The frontal glabellar lobe is slightly swollen, but not notably wider than the succeeding lobes which are delimited by shallow transglabellar furrows. The occipital ring is roughly triangular, the mesial part protruding as a blunt node in posterior direction. A preglabellar field is well-developed. The palpebro-ocular ridge is long and wide, strongly curved, anteriorly flaring and joining the frontal glabellar lobe along its entire length. The genae are moderately arched; finer prosopon structures are not preserved.

**Affinities.** – The type species *Holmia kjerulfi* is by far the best known species of the genus as the available material of other species usually is strongly fragmented. *Holmia hyperborea* n. sp. differs in some respects distinctly from other *Holmia* species, but in other respects the new species shows features believed to be diagnostic of the genus. These features include general glabellar morphology, advanced genal spines, intergenal spines close to the occipital ring, sixteen segments in the thorax which is considerably narrower anteriorly than the cephalon, strongly deflected pleurae, and narrow extra-ocular genae.

Fritz (1973, p. 13) moved the species *mirabilis* from *Holmia* to *Wanneria*? in a discussion of *Holmia* and *Holmia*-like species, but the advanced genal spines and general resemblance to *Holmia hyperborea* n. sp., which has a holmiid thorax very much different from that of *Wanneria*, make an assignment to *Wanneria* very unlikely.

Bergström (1973, p. 287) excluded *Holmia mirabilis* Poulsen from *Holmia* because of the notably convex cephalic border, and he (1973, p. 306) does not attach generic importance to advanced genal spines. I do not agree with Bergström with regard to the significance, respectively insignificance of these features, and to restrict *Holmia* to include a few Scandinavian and Baltic species prevents all possibilities of getting an idea of holmiid variation. I believe that the bent posterior cephalic margin in *Holmia kjerulfi* is real, and not partly an effect of postdepositional compression; the advanced genal angle then is a primary feature. The relative convexity of the cephalic border is a function of border width, and differences in border width have now been shown to have importance only at the species level within the olenel-



laceans (e.g. *Olenellus* and *Holmia*). Accordingly, *Holmia mirabilis* is here included in *Holmia*, and the statistical evaluation (see later on) seems to justify this procedure.

*Holmia hyperborea* n. sp. differs from the type species, *Holmia kjerulfi*, in having a narrower cephalic border, more advanced genal spines, a less prominent frontal glabellar lobe just touching anterior border furrow, and a thorax with longer pleural spines which smoothly join the deflected part of the pleurae. Also statistical comparisons, showing significant differences, have been carried out (see below). The same criteria for distinction apply to other Scandinavian and Baltic species which have been assigned to *Holmia*. Some of the olenellacean species have been revised by Bergström (1973).

*Holmia mirabilis* described by C. Poulsen (1958) from western North Greenland and *Holmia argenta* (Walcott) from Nevada appear to be the morphologically closest relatives of *Holmia hyperborea* n. sp. The Nevada species was erected by Walcott (1910) as *Olenellus? argentus*, but as suggested by Fritz (1972, p. 13) this species should be placed under *Holmia* (not including the cephalon in Walcott's pl. 40, fig. 14, which may be a *Holmiella*). Both species, of which only the cephalon are known, differ from *Holmia hyperborea* n. sp. in the less advanced genal spines, wider cephalic border, and more strongly expanded frontal glabellar lobe associated with a narrowing of anterior border in front of the glabella.

*Holmia mobergi* Bergström, 1973 differs from *Holmia hyperborea* n. sp. in possessing genal angles aligned with the almost straight posterior cephalic border, and by having a frontal glabellar lobe which "pushes" into the narrow anterior border, and by the wider lateral cephalic border. *Holmia sulcata* Bergström, 1973 resembles *Holmia hyperborea* n. sp. somewhat with regard to the course of the glabellar furrows, but differs entirely in morphology of the frontal glabellar lobe and of anterior border in front of it, and no shallow longitudinal furrow is present in the cephalic border as in *Holmia hyperborea* n. sp. (see for instance pl. 3, figs. 3 and 4).

*Holmia hyperborea* n. sp. differs from *Holmia?* sp. 1 described by Fritz (1973) in having the genal spines in a more advanced position and by having a simple occipital ring.

Remarks. — The four available meraspid cephalon of *Holmia hyperborea* n. sp. all belong to the same morphological stage and strongly resemble a meraspid cephalon of *Holmia kjerulfi*, figured by Kiær (1916, pl. VIII, fig. 2). Kiær did not indicate the presence of procranial spines and long intergenal spines; they were most likely developed, but are not preserved in the Norwegian material. The occurrence of procranial spines in developmental stages of *Holmia hyperborea* n. sp., where genal as well as intergenal spines are present, supplements Palmer's (1957) observations on *Olenellus*

*gilberti* and *Olenellus clarki*, showing that the genal spines cannot be derived from the procranial spines.

### Statistical analysis

A statistical treatment of the *Holmia* material has been undertaken to get more information about the growth functions and for comparison with *Olenellus*. The ontogenetic development of olenellacean trilobites is not too well known, and published quantitative studies of the ontogeny are rare. Palmer (1957) studied the ontogeny of *Olenellus gilberti* and *Olenellus clarki* (formerly assigned to *Paedeumias*) in a large silicified material from the Combined Metals Bed of the Pioche Shale in Nevada.

The growth functions may be regarded as important and for some features most likely diagnostic, at least at the species level; therefore the new species of *Holmia* has been compared statistically with *Olenellus* using data published by Palmer (1957, p. 108).

### Procedure and choice of methods

The *Holmia* specimens are flattened and slightly distorted, but the amount of distortion is judged to be of no importance for the statistical evaluations, as the product-moment correlation coefficients for all the calculated regressions attain highly significant values at the 0.01 level.

Measurements were made with an ocular micrometer, 1 mm being equal to 7.7 micrometer divisions at approximately 7.5 times magnification. The principal measurements are shown in fig. 2 and are listed in table 1, p. 90. The statistical methods used are those recommended by Shaw (1956), Imbrie (1956), and Simpson et al. (1960).

A scatter plot of the raw data in several instances (see fig. 3) suggests a curvilinear relationship, as the extreme Y values show a positive deviation from the "best fit" line, while intermediate Y values tend to show a negative deviation. This relationship and the fact that the "best fit" line does not pass through the origin indicate a faint allometric growth and, accordingly, the corresponding logarithmic values of the variates are used in the scatter diagrams for calculation of the regressions, and for the statistical tests. A 5 % fiducial level has been used in all the tests of differences between samples.

Bartlett's method to find the straight line, which presents the best fit to the variates, is recommended by Simpson et al. (1960), and this method has been tried and compared to the method of the "reduced major axis" recommended by Imbrie (1956). With a reasonably large number of observations the resulting equations are for all purposes identical, but the "reduced major axis" method has been chosen here, as the number of observations is

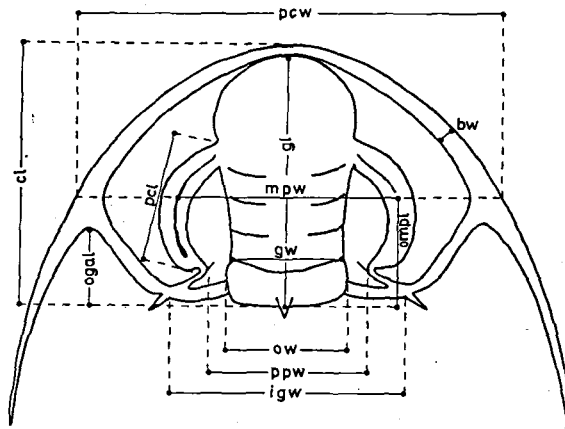


Fig. 2. Diagram showing the principal cephalic measurements, partly according to Shaw (1957). *bw* = Border width opposite anterior end of palpebro-ocular ridge. *cl* = Cephalic length without spines. *gl* = Glebellar length including occipital ring. *gw* = Width of glabella at base. *igw* = Width between intergenal spines. *mpw* = Width between midpoints of palpebro-ocular ridges (Bergström, 1973). *oga* = Position of advanced genal spines, measured as the distance between genal angle and cephalic base line. *ompl* = Occipital mid-palpebral length measured from cephalic base line along the sagittal plane to the projection of the palpebral midpoint, this being the best measure of the eye position. *ow* = Width of occipital ring. *pcl* = Length of palpebro-ocular ridge measured directly along the chord. *pcw* = Cephalic width measured along a transverse line passing through the palpebral midpoints; in *Holmia hyperborea* n. sp. this measurement in most instances coincides with the maximum width of the cephalon (excluding spines). *ppw* = Width between posterior extremities of palpebro-ocular ridges.

restricted in several instances. Bartlett's method requires a tripartite, ascending grouping of the data, and the slope is calculated from the sample means for the lowest and highest groups only. The Y intercept is then obtained from an expression involving the slope and the grand means of the sample variates.

In trilobites the growth functions may have changed considerably from the protaspid to the meraspid stage and from the meraspid to the holaspid stage, and using Bartlett's method, especially on small samples, the result may be strongly biased. Thus Palmer (1957, figs. 3C-D and 4A-B) has demonstrated distinct changes in the growth functions during the early ontogeny of *Olenellus*.

All the sample variates are involved in the calculation of the "reduced major axis", thereby reducing the possible bias in small samples. However, possible changes in the growth functions during the ontogeny have not been taken into account here, as an evident overlap in size of different instars

Table 1. Cephalic measurements in mm of 25 specimens of *Holmia hyperborea* n. sp. from Børglum Elv. See text-fig. 2 for explanation of symbols. m = meraspid, h = holotype.

	cl	pcw	gl	gw	ow	igw	pcl	mpw	ppw	bw	ogal	ompl
m	1.62	1.79	1.17	0.26	—	0.39	0.79	0.81	—	0.13	0.36	0.65
m	1.95	2.86	1.46	0.52	0.65	1.43	0.91	1.43	1.36	0.18	0.45	0.84
m	2.08	3.12	1.53	0.52	—	1.49	0.91	1.56	1.09	0.16	0.53	0.85
m	2.66	3.77	2.14	0.58	—	1.56	1.30	1.82	1.43	0.19	0.65	1.04
	4.16	6.49	3.44	1.43	1.56	3.12	1.69	3.25	2.34	0.32	1.23	1.82
	4.68	7.51	3.83	1.56	1.88	3.96	1.95	3.57	2.66	0.26	0.91	1.75
h	4.68	8.05	3.89	1.88	1.95	4.55	2.34	3.96	2.86	0.38	1.36	1.82
	4.74	7.40	4.17	1.68	1.88	3.64	2.08	3.64	2.73	0.34	1.17	1.95
	4.87	8.57	4.35	1.95	—	4.42	2.34	4.42	3.12	0.32	1.40	2.08
	6.69	11.43	6.36	2.98	3.11	6.75	3.25	5.97	3.77	0.45	2.34	2.93
	—	11.17	—	—	—	—	3.18	5.71	—	0.32	—	—
	6.75	11.04	5.60	2.60	2.79	6.10	2.86	5.13	3.77	0.36	1.17	2.60
	6.75	11.42	5.58	—	—	6.49	2.79	5.32	4.55	0.41	1.95	2.66
	—	11.69	—	—	—	6.49	3.64	5.19	—	0.39	1.56	2.99
	7.79	14.03	—	3.11	3.76	7.40	3.12	6.49	4.16	—	1.69	3.25
	7.53	12.98	6.82	3.37	3.90	7.66	3.57	5.71	3.77	0.45	2.60	3.31
	8.57	—	7.46	3.77	4.16	8.83	4.20	7.53	4.94	0.48	—	3.51
	9.09	—	8.44	2.60	—	7.79	3.77	7.01	—	—	—	2.73
	—	15.32	—	—	—	—	—	8.05	—	0.58	—	—
	10.52	16.23	9.15	4.16	4.42	9.35	4.28	7.92	6.10	0.55	2.60	4.68
	10.78	17.01	9.67	4.02	5.45	9.87	5.13	8.57	6.10	0.52	3.12	4.15
	—	—	—	5.19	5.58	10.78	4.93	9.61	—	—	—	3.90
	—	22.08	—	—	5.84	12.20	—	10.26	7.14	—	—	4.55
	—	—	—	—	—	—	—	10.90	—	—	—	—
	—	26.49	—	—	5.84	16.62	—	13.51	8.31	—	—	—

in most cases prevents an analysis of the individual developmental stages. Besides, the correlation coefficients for the bulk samples in all instances attain highly significant values.

Palmer (1957) analysed the overall changes in cephalic morphology of *Olenellus gilberti* and *Olenellus clarki* using a modified D'Arcy Thompson grid, and it appeared that the glabellar length and the distance between the palpebral lobes remained nearly proportional with increasing size. Accordingly, the glabellar length is here used throughout as one of the variates to which other cephalic dimensions are compared. Palmer concluded that the relative width of the border was a diagnostic feature separating *Olenellus* from *Paedeumias*, but this is not so according to additional olenellid material obtained by Palmer (1973, oral communication).

The proximal position of the intergenal spines and the advanced genal

angles are considered to be of diagnostic importance in *Holmia*, and these features, as well as cephalic border width, and the distance between the palpebro-ocular ridges posteriorly have also been selected for statistical studies.

#### Comparison of *Holmia hyperborea* n. sp. to other species of *Holmia*

Regressions of log values of intergenal width, border width, distance between posterior extremities of palpebro-ocular ridges (Bergström, 1973), and position of the advanced genal spines on the glabellar length have been calculated for *Holmia hyperborea* n. sp. (figs. 3-7) from the data presented in table 1. The corresponding regressions for *Holmia kjerulfi* have been calculated from the data in table 2, based on the figured specimens in Kiær (1916, pl. VI-VIII).

*Holmia mirabilis* from western North Greenland appears to be a close relative of *Holmia hyperborea* n. sp. (see p. 86), and important cephalic dimensions of the two known specimens have been tested in the regressions calculated for *Holmia hyperborea* n. sp. and the type species, *Holmia kjerulfi* (see figs. 3-7). The log values of the variates in *Holmia mirabilis* were

Table 2. Cephalic measurements in mm of *Holmia kjerulfi* from Norway (data from Kiær, 1916) and *Holmia mirabilis* from western North Greenland. Only measurements used in statistical analyses are shown. See text-fig. 2 for explanation of symbols. m = meraspid.

		gl	igw	ppw	bw	ogal
<i>Holmia kjerulfi</i>	m	3.25	-	-	0.25	0.63
		5.38	-	-	0.54	0.38
		9.00	8.00	5.80	1.25	1.50
		13.50	11.00	8.60	1.50	1.00
		14.50	14.20	9.50	1.50	2.00
		15.50	17.00	11.70	1.50	2.00
		24.00	27.00	21.80	2.50	3.50
		27.50	30.00	28.00	3.50	5.00
		15.45	15.70	11.60	2.00	3.00
		11.50	11.00	7.30	1.20	1.00
		12.00	-	-	1.25	1.00
		15.00	15.00	11.60	1.75	1.50
		14.50	15.00	10.00	2.00	1.00
		14.50	18.00	12.50	1.50	2.00
		19.50	20.00	-	2.50	3.00
<i>Holmia mirabilis</i>		3.20	3.77	3.12	0.39	0.39
		6.29	8.05	4.68	1.04	1.30

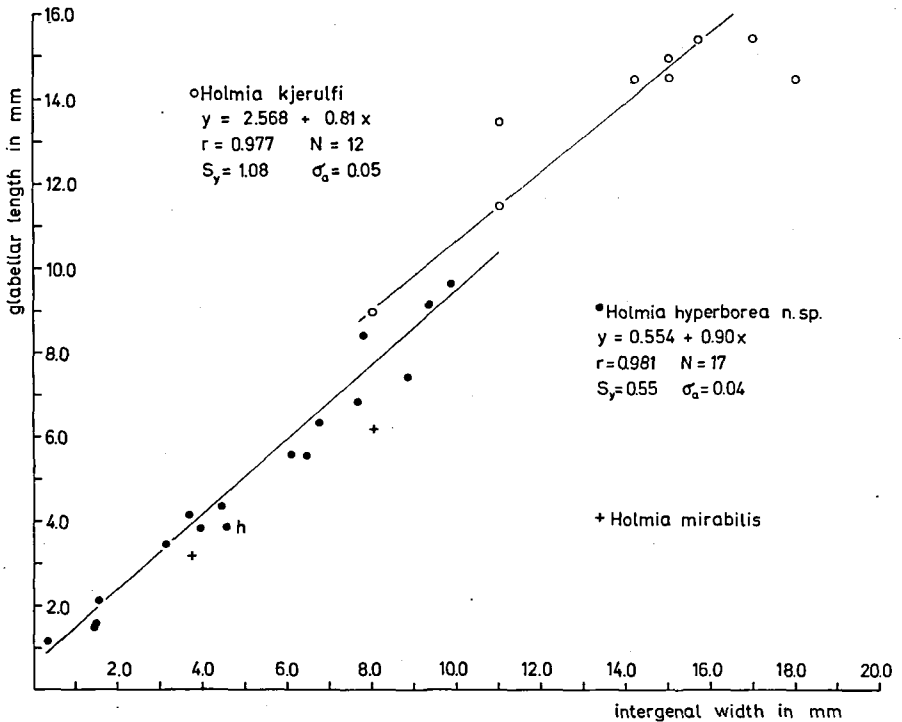


Fig. 3. Scatter plot of glabellar length (gl) and width between intergenal spines (igw) in mm in *Holmia hyperborea* n. sp. (dots), *Holmia kjerulfi* (open circles, not all variates shown) and *Holmia mirabilis* (crosses). Intermediate Y value in *Holmia hyperborea* n. sp. show negative deviation, whereas extreme Y values tend to show positive deviations, thereby suggesting a faint allometric growth. Regressions are calculated by the "reduced major axis" method. N = number of pairs of observations. r = product-moment correlation coefficient.  $S_y$  = standard error of estimate.  $\sigma_a$  = standard error of slope. h = holotype of *Holmia hyperborea* n. sp. The data are listed in tables 1 and 2, pp. 90–91.

substituted in the regression equations for *Holmia hyperborea* n. sp. and *Holmia kjerulfi*, and then the differences between the observed and calculated values of log glabellar lengths were tested for significance by means of the standard error of estimate according to Shaw (1966, pp. 1222–1223).

*Holmia mirabilis* differs in most instances significantly from the two other species of *Holmia*. Exceptions when compared to *Holmia hyperborea* n. sp. are the intergenal width and the distance between the palpebro-ocular ridges posteriorly in the large specimen, and compared to *Holmia kjerulfi* the two specimens of *Holmia mirabilis* show no significant difference in position of the advanced genal spines.

The differences between the regression lines for *Holmia hyperborea* n. sp. and *Holmia kjerulfi* (figs. 3–7) have also been tested for significance. The

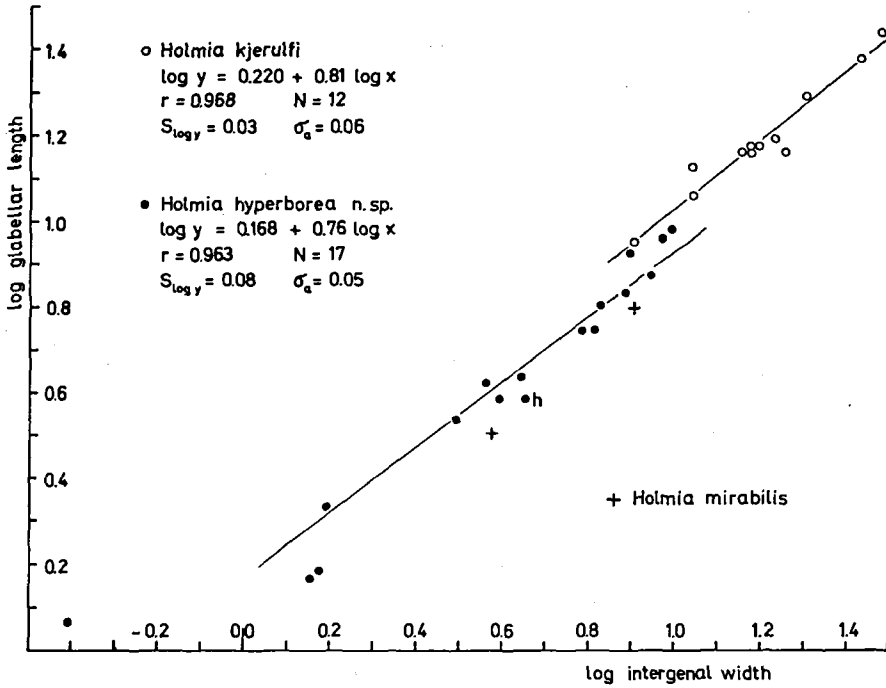


Fig. 4. Scatter plot of the logarithmic values of the measurements presented in fig. 3. Same symbols as in fig. 3.

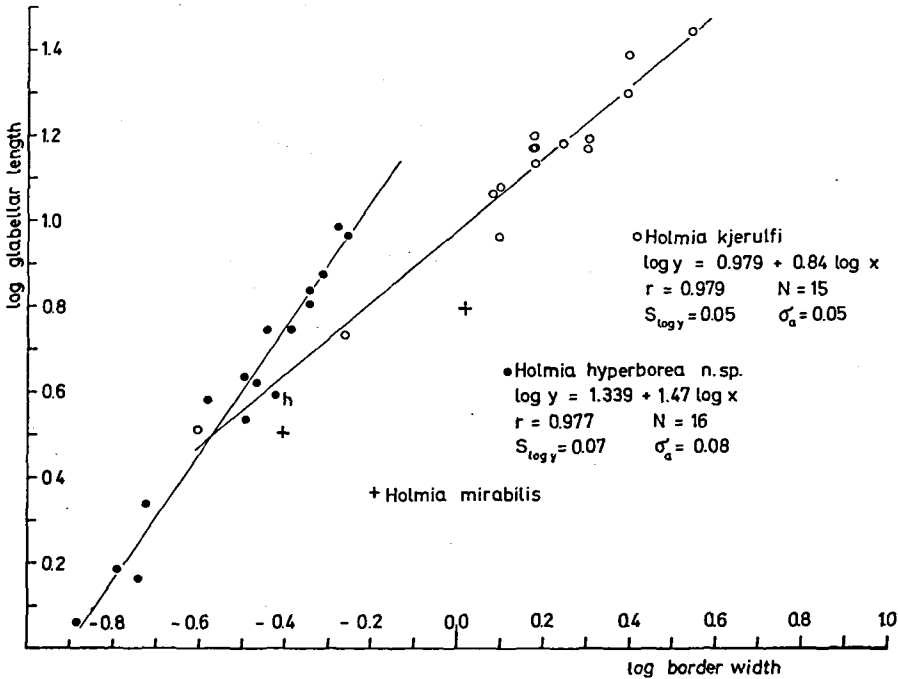


Fig. 5. Scatter plot of the log values of glabella length (gl) and width of cephalic border (bw) in *Holmia hyperborea* n.sp. (dots), *Holmia kjerulfi* (open circles), and *Holmia mirabilis* (crosses). Symbols as in fig. 3.

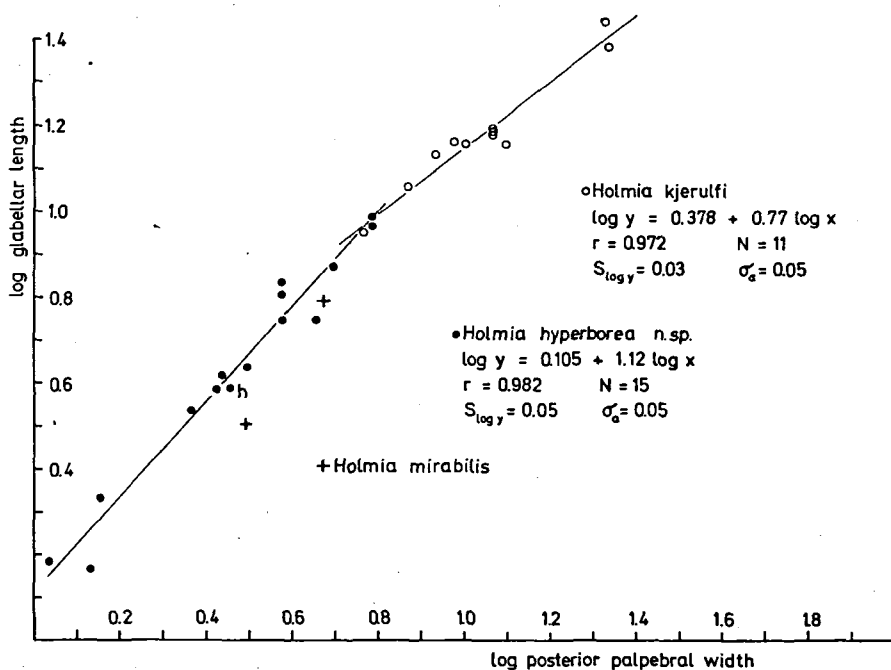


Fig. 6. Scatter plot of the log values glabellar length (gl) and distance between posterior extremities of palpebro-ocular ridges (ppw) in *Holmia hyperborea* n. sp. (dots), *Holmia kjerulfi* (open circles), and *Holmia mirabilis* (crosses). Symbols as in fig. 3.

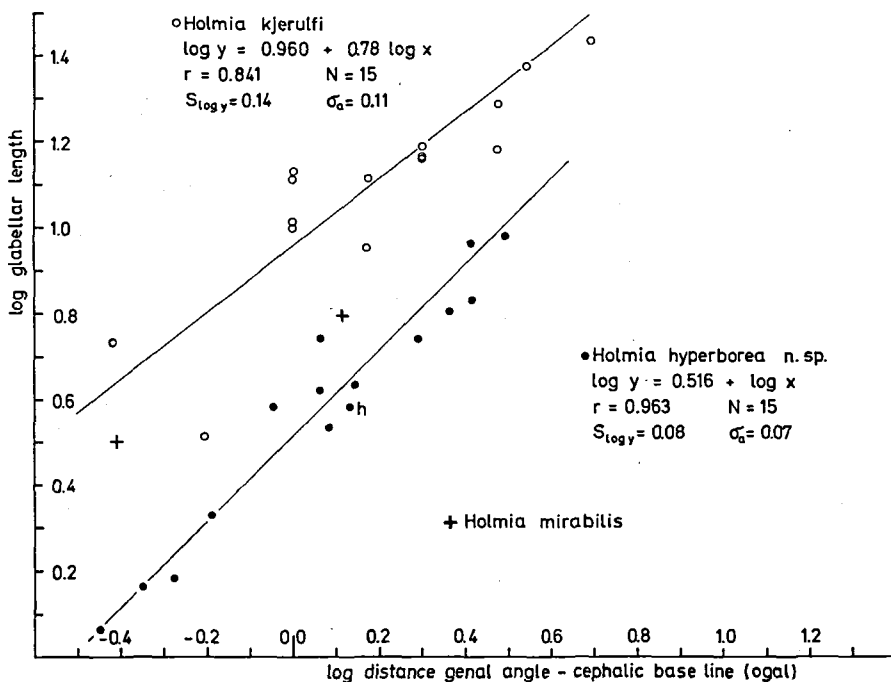


Fig. 7. Scatter plot of the log values of glabellar length (gl) and position of the advanced genal spines (ogal) in *Holmia hyperborea* n. sp. (dots), *Holmia kjerulfi* (open circles), and *Holmia mirabilis* (crosses). Symbols as in fig. 3.



difference in slope is tested by the standard error of the difference between the two coefficients of regression (Shaw, 1956, p. 1219), and where no significant difference is evident, the position of Y intercept may be analysed, assuming that the slopes of the lines for the original populations actually differ and that the observed difference is an estimate of the true differences (Imbrie, 1956, p. 237).

The slope difference between the regression lines for intergenal width on glabellar length is not significant ( $t = 0.384$ .  $0.7 < P < 0.8$  with 25 degrees of freedom). The difference in Y intercept is regarded as significant ( $z = 3.758$ ) although the number of observations is slightly below the desired minimum ( $N_1 + N_2 = 35$  or more).

The analyses of border width, distance between palpebro-ocular ridges and position of the advanced genal angles in *Holmia hyperborea* n. sp. and *Holmia kjerulfi* have been carried out in the same way, and the difference in slope is highly significant with regard to the border width and distance between the palpebro-ocular ridges, and significant for the position of the advanced genal angles.

It is concluded that the border width may be important for distinction at the specific level, whereas the other characters require a careful evaluation. The proximal position of the intergenal spines is still considered to be diagnostic of *Holmia*, but despite similar growth patterns within the observed range, as demonstrated by *Holmia hyperborea* n. sp. and *Holmia kjerulfi*, differences in the initial growth index (Y intercept) may occur.

#### Comparisons of *Holmia* to *Olenellus*

Regressions for border width, intergenal width and distance between the palpebro-ocular ridges on the glabellar length have been calculated for *Olenellus gilberti* and *Olenellus clarki* (figs. 8–10) using the logarithmic values of the data published by Palmer (1957, table 1, p. 108). The genal angles in *Olenellus* are roughly aligned with the straight posterior border of cephalon, and the position of the genal angles has not been tested statistically, partly because no data were available for *Olenellus*, and partly because the positional differences from *Holmia* may be considered to be diagnostic and easily recognized at a glance.

The length of the intergenal spines in *Olenellus* was analysed by Palmer (1957), but as this feature is very often obscured by an imperfect state of preservation no quantitative studies of the spine length have been undertaken.

The analysis of the regression line for border width in *Holmia hyperborea* n. sp. shows a highly significant difference in slope from *Olenellus* (fig. 8), whereas there is no significant difference between the slope for *Olenellus* and *Holmia kjerulfi*, and between the two species of *Olenellus*. In these in-

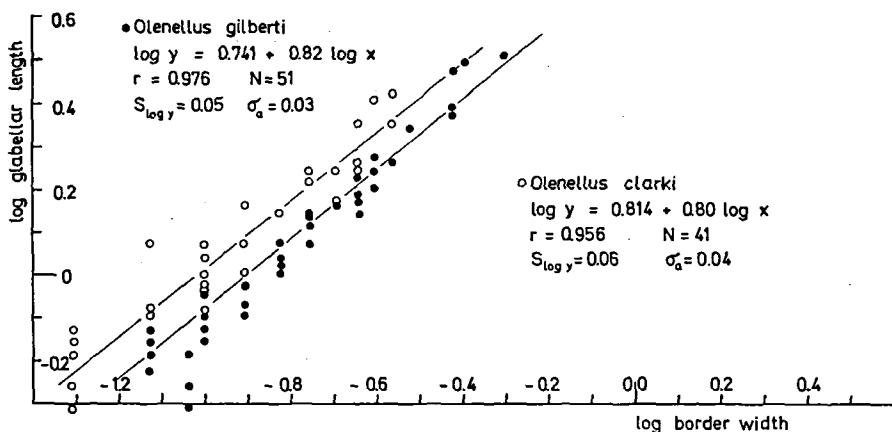


Fig. 8. Scatter plot of the log values of glabella length (gl) and width of cephalic border (bw) in *Olenellus gilberti* (dots) and *Olenellus clarki* (open circles). Repetitions of identical values are not shown. Data from Palmer, 1957. Symbols as in fig. 3.

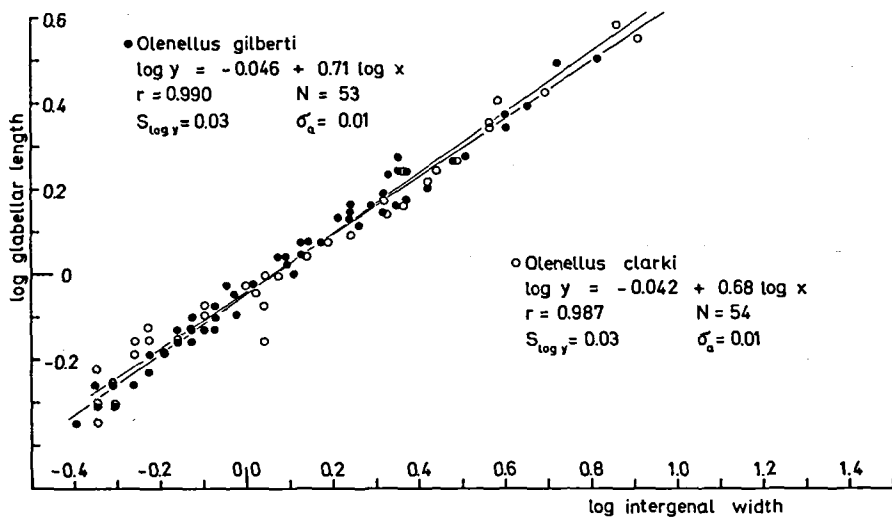


Fig. 9. Scatter plot of the log values of glabella length (gl) and distance between intergenal spines (igw) in *Olenellus gilberti* (dots) and *Olenellus clarki* (open circles). Repetitions of identical values are not shown. Data from Palmer, 1957. Symbols as in fig. 3.

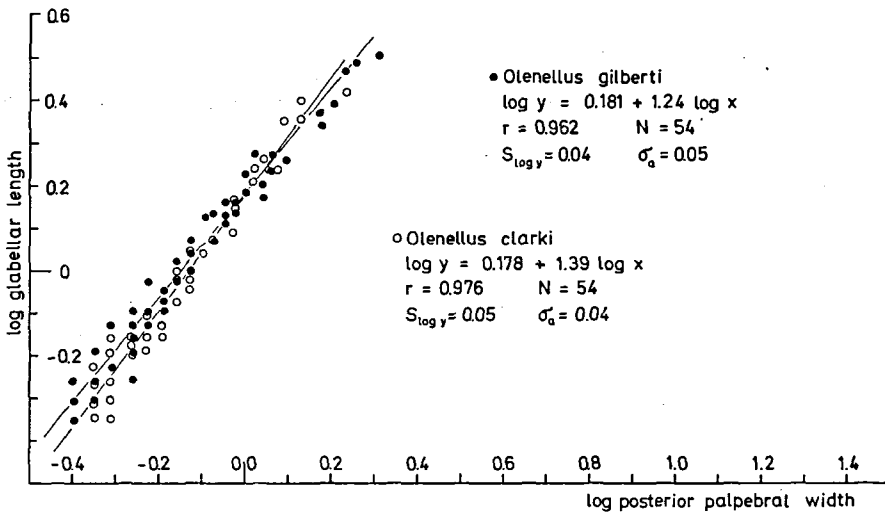


Fig. 10. Scatter plot of the log values of glabellar length (gl) and distance between palpebro-ocular ridges posteriorly (ppw) in *Olenellus gilberti* (dots) and *Olenellus clarki* (open circles). Repetitions of identical values are not shown. Data from Palmer, 1957. Symbols as in fig. 3.

stances, however, a highly significant difference is found in the initial growth index (Y intercept).

There is a significant or almost significant difference between *Olenellus clarki* and the two species of *Holmia* in the growth pattern of the intergenal width (fig. 9), whereas the slope of the regression lines does not appear to be statistically different between *Holmia* and *Olenellus gilberti*. Highly significant differences are found between *Holmia* and the Nevada species with regard to the initial growth index. There appears to be no statistically significant difference between the two species of *Olenellus* in slope or initial growth index.

Testing the distance between the palpebro-ocular ridges a highly significant difference in regression coefficients as well as in initial growth index (fig. 10) is found between *Olenellus* and *Holmia kjerulfi*. As for *Holmia hyperborea* n. sp. a highly significant difference from *Olenellus clarki* is seen in the slope, and an almost significant difference ( $z = 1.921$ ) from *Olenellus gilberti* in the initial growth index.

It appears that the growth patterns reflected by the regression coefficients for the analysed variables in quite a few instances fail to show any statistically significant difference at the generic level, and a similarity in this respect is only to be expected among the only moderately differentiated olenelaceans. On the other hand highly significant differences in slope of the structural lines may be found at the specific level, e.g. border width and

distance between the palpebro-ocular ridges in *Holmia hyperborea* n. sp. and *Holmia kjerulfi*.

The difference between the initial growth indices appears to be highly significant in most cases, not only at the generic level but also at the specific level, e.g. intergenal width in the two species of *Holmia*.

### Instars

Palmer (1957, pp. 110–114) discussed instars of *Olenellus gilberti* and *Olenellus clarki*, and using different approaches the growth factor and the number of molts were calculated. He found the growth factor (average) to be 1.13 for *Olenellus gilberti* and 1.16 for *Olenellus clarki*.

The size ranges of the specimens of *Holmia hyperborea* n. sp. suggest the possible presence of 5 instars (fig. 11), and by using the percentage increase in cephalic length for successive instars the growth factor may be roughly estimated. A growth factor of 1.55 seems to fit the observations best, and by multiplying the average cephalic length in the smallest instar by 1.55 the following values in mm are obtained for the subsequent instars (with observed averages in brackets): 2.91 (2.66), 4.52 (4.63), 7.00 (7.10), and 10.85 (10.65).

The array of plots in fig. 11 suggests that the growth functions within the separate instars are somewhat different from the "best fit" line calculated

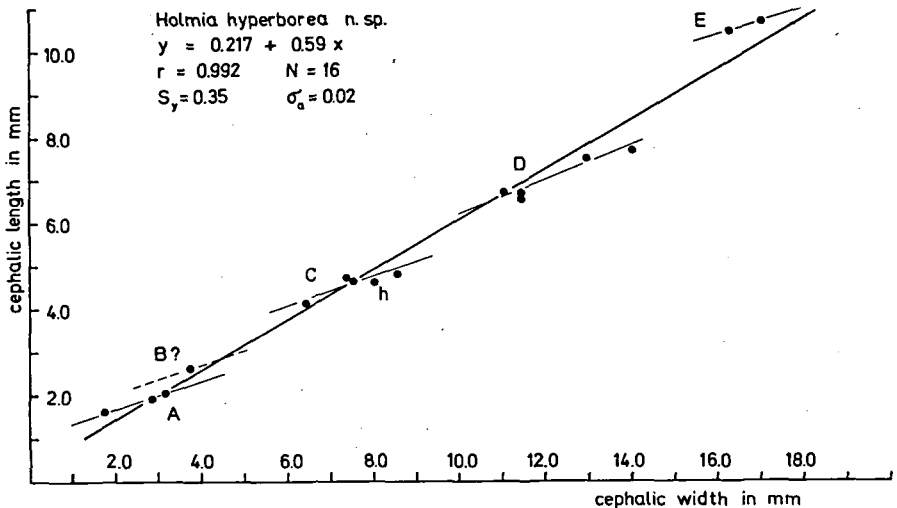


Fig. 11. Scatter plot of cephalic length (cl) and cephalic width (cw) in mm in 16 specimens of *Holmia hyperborea* n. sp. Data from table 1, p. 90. The array suggests the presence of 5 instars A–E. Instar C represents an early holaspide stage. Structural lines fitted to the separate instars have regression coefficients about 0.34, much lower than the one calculated for the bulk sample. Symbols as in fig. 3.

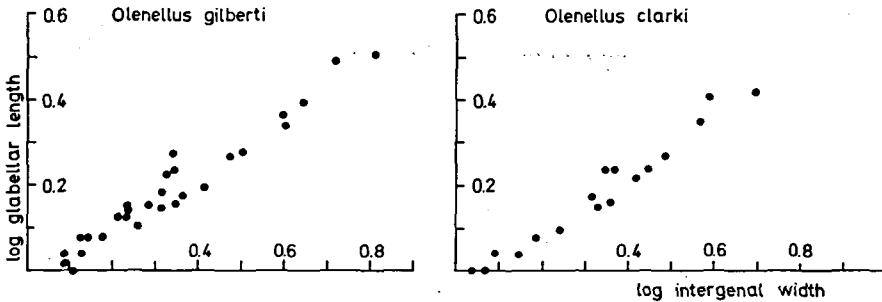


Fig. 12. Scatter plot of log values of glabella length (gl) and distance between intergenal spines (igw) in *Olenellus gilberti* and *Olenellus clarki*. Only specimens with glabella lengths exceeding 1 mm are shown. The plume-like array of the variates in both genera may indicate a growth pattern similar to that of *Holmia hyperborea* n. sp. (shown in fig. 11). Data from Palmer, 1957.

for the entire sample ( $y = 0.217 + 0.59 x$ ), as the slope of the lines for the separate instars is about 0.34. The same pattern appears when the logarithmic values of the variates are used.

A similar relationship is quite evident in other scatter diagrams. The plume-like array in scatter diagrams of distance between intergenal spines on glabella length in *Olenellus* (data from Palmer, 1957), especially using the logarithmic values of the variates (fig. 12), suggests that growth functions in the separate instars with glabella lengths exceeding 1 mm also may differ from that estimated for the bulk samples. The appearance of the "plume" at a stage where major changes in the growth pattern are evident (Palmer, 1957, p. 110) may be significant; the changes occur in *Olenellus* when the glabella length approaches 1 mm.

The fitting of structural lines to separate instars might provide more detailed information about the ontogeny, which would be of possible value for taxonomic inferences. However, samples of trilobite growth series are commonly either too small to secure reliable regressions, or too large to permit a clear distinction between the instars due to the size overlap.

## Dansk sammendrag

Et materiale af olenellide trilobiter indsamlet af Troelsen i 1949 ved Schley Fjord inden for det nordgrønlandske foldebælte (fig. 1) beskrives for første gang. Materialet rummer kun *Olenellus* cf. *svabardensis*. Bevaringstilstanden tillader ikke en endelig placering; men det er overvejende sandsynligt, at det må være den art, som er beskrevet fra Hornsund, Spitsbergen. Ligeledes beskrives en ny art af *Holmia* i et materiale indsamlet fra Børglum Elv, Peary Land (fig. 1). Dette materiale er indsamlet af Greenarctic Consortium og skænket til Grønlands Geologiske Undersøgelse. *Holmia*-materialet repræsenterer flere vækststadier, som er behandlet statistisk og sammenlignet

med arter af *Olenellus* fra Nevada, analyseret af Palmer (1957). Arten *clarki* er flyttet fra *Paedeumias* til *Olenellus*, og meget taler for, at *Paedeumias* ikke kan opretholdes som en selvstændig slægt, hvad der tildels fremgår af den statistiske analyse.

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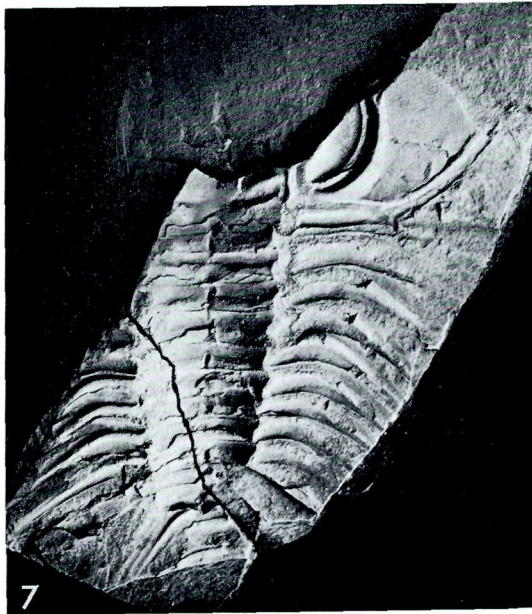
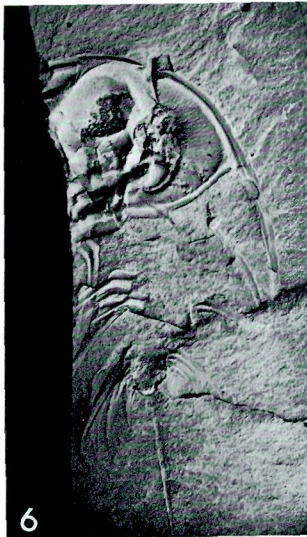
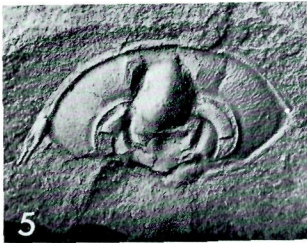
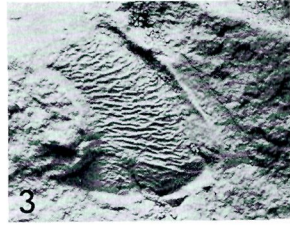
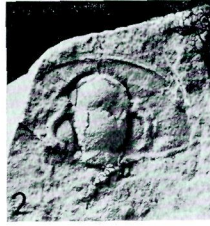
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## Plate 1

- Figs. 1–3. *Olenellus* cf. *svalbardensis* Kielan, 1960 ..... page 82
- 1: Internal mould of incomplete exoskeleton (MMH no. 13005). × 2.
  - 2: Internal mould of incomplete cephalon (MMH no. 13006). × 2.
  - 3: Internal mould of extraocular gena showing genal prosopon (MMH no. 13007). × 2.
- Figs. 4–7. *Holmia hyperborea* n. sp. .... page 84
- 4: Ventral view of a small, almost complete holaspid exoskeleton. Holotype (MMH no. 13008). "Photographic replica". × 3.
  - 5: Almost complete cephalon (MMH no. 13009). × 3.
  - 6: Ventral view of incomplete cephalon and posterior part of thorax showing outline of pygidium (MMH no. 13010). "Photographic replica". × 3.
  - 7: Ventral view of incomplete cephalon and thorax (MMH no. 13011). "Photographic replica". × 3.

All figured specimens are whitened with antimony. The photographs are not retouched. "Photographic replicas" (figs. 4, 6 and 7) of specimens in ventral view are optical illusions produced by the light coming from the lower right corner. The specimens of *Holmia hyperborea* n. sp. are from GGU collection 100824.



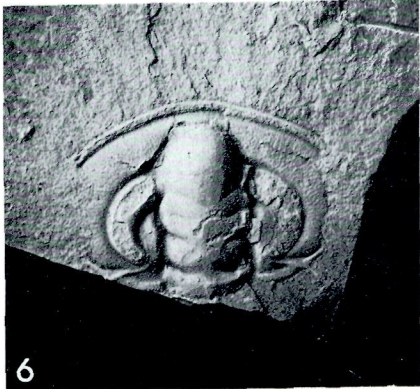
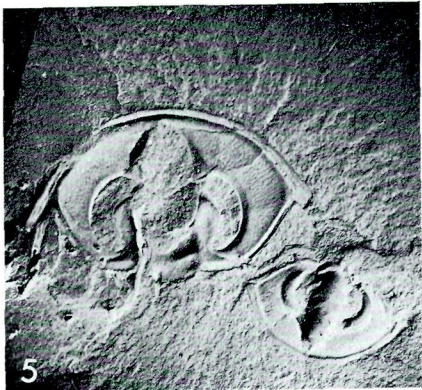
## Plate 2

Figs. 1-6. *Holmia hyperborea* n. sp. . . . . page 84

- 1: Small cephalon (MMH no. 13012).  $\times 3$ .
- 2: Ventral view of small cephalon (MMH no. 13013). "Photographic replica".  $\times 3$ .
- 3: Almost complete cephalon (MMH no. 13014).  $\times 3$ .
- 4: Ventral view of incomplete cephalon and thorax (MMH no. 13015). "Photographic replica".  $\times 3$ .
- 5: Incomplete cephalon (MMH no. 13016).  $\times 3$ . The small cephalon in the lower right corner is also shown in pl. 2, fig. 2.
- 6: Incomplete cephalon (MMH no. 13017).  $\times 3$ .

All figured specimens, which are from GGU collection 100824, are whitened with antimony. The photographs are not retouched. "Photographic replicas" (figs. 2 and 4) of specimens in ventral view are optical illusions produced by the light coming from the lower right corner.



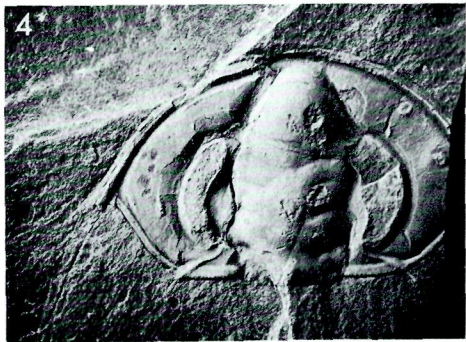


### Plate 3

Figs. 1-8. *Holmia hyperborea* n. sp. . . . . page 84

- 1: Oblique dorsal view of an incomplete exoskeleton (MMH no. 13018) which is bent sideways, with all pleural spines joining in a tight bundle.  $\times 3$ .
- 2: Almost complete cephalon (MMH no. 13019).  $\times 3$ .
- 3: Almost complete cephalon (MMH no. 13020).  $\times 3$ .
- 4: Almost complete cephalon (MMH no. 13021).  $\times 3$ .
- 5: Oblique dorsal view of meraspid (MMH no. 13022) showing long intergenal spine.  $\times 10$ .
- 6: Incomplete meraspid (MMH no. 13023).  $\times 10$ .
- 7: Ventral view of meraspid (MMH no. 13024). "Photographic replica".  $\times 10$ .
- 8: Ventral view of meraspid (MMH no. 13025). "Photographic replica".  $\times 10$ .

All figured specimens, which are from GGU collection 100824, are whitened with antimony. The photographs are not retouched. "Photographic replicas" (figs. 7 and 8) of specimens in ventral view are optical illusions produced by the light coming from the lower right corner.



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