

Phenotypic variation in the Middle Cambrian trilobite *Paradoxides davidis* SALTER at Manuels, SE Newfoundland.

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with 11 Textfigures, 2 Tables and 10 Plates

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The type subspecies *Paradoxides davidis davidis* recurs at least three times in the dominantly silty rock column. The first intervening interval contains *P. d. trapezopyge* n. ssp., followed by *P. d. intermedius* n. ssp.. The latter may be a hybrid between the former and *P. d. davidis*. The last intervening interval contains *P. d. brevispinus* n. ssp.. The number of thoracic tergites varies within subspecies. Teratologies affect *P. d. trapezopyge* and *P. d. intermedius*. The onset of subspecies ranges is correlated with diastems. The differentiation of new subspecies may be local and allopatric. The type subspecies may have been morphologically static and capable of intermittent immigration. Our evidence conforms with the predictions of the model of punctuated equilibria. *P. forchhammeri* may have evolved directly from one of the *P. davidis* subspecies.

P. davidis tritt in mindestens 3 getrennten Niveaus in einer überwiegend siltigen Folge auf. Zwischen dem 1. und 2. Auftreten erscheint *P. d. trapezopyge* n. ssp., über der *P. d. intermedius* n. ssp. folgt. Letztere könnte ein Hybrid zwischen *P. d. d.* und *P. d. t.* sein. Zwischen dem 2. und 3. Auftreten von *P. d. d.* kommt *P. d. brevispinus* n. ssp. vor. Die Zahl der Thoracalergiten variiert innerhalb der Unterarten. Teratologische Erscheinungen treten bei *P. d. t.* und *P. d. i.* auf. Die Unterarten könnten lokal allopatrisch entstanden sein. *P. d. davidis* könnte morphologisch »statisch« geblieben, daher zu wiederholten Einwanderungen imstande gewesen sein. Die Befunde stehen mit dem Modell von »punctuated equilibria« in Einklang. *P. forchhammeri* könnte direkt von einer der *P. davidis*-Unterarten stammen.

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Stratigraphic distributions at Manuels, Newfoundland.

The Lower and Middle Cambrian sequence at Manuels on the Avalon Peninsula, eastern Newfoundland, and its fossils were studied in detail by HOWELL (1925). The fossil faunas were later revised by HUTCHINSON (1962). The *Paradoxides davidis* beds include HOWELL's beds 93 through 125, comprising roughly 9.4 m (31 feet) of sediments according to HOWELL. HOWELL measured this part of the section on the west side of Manuels River. During five field trips in 1974–1977, we have systematically explored the top four meters of the *P. davidis* beds, on the east side of the manuels River. These correspond to HOWELL's bed 110 through 125.

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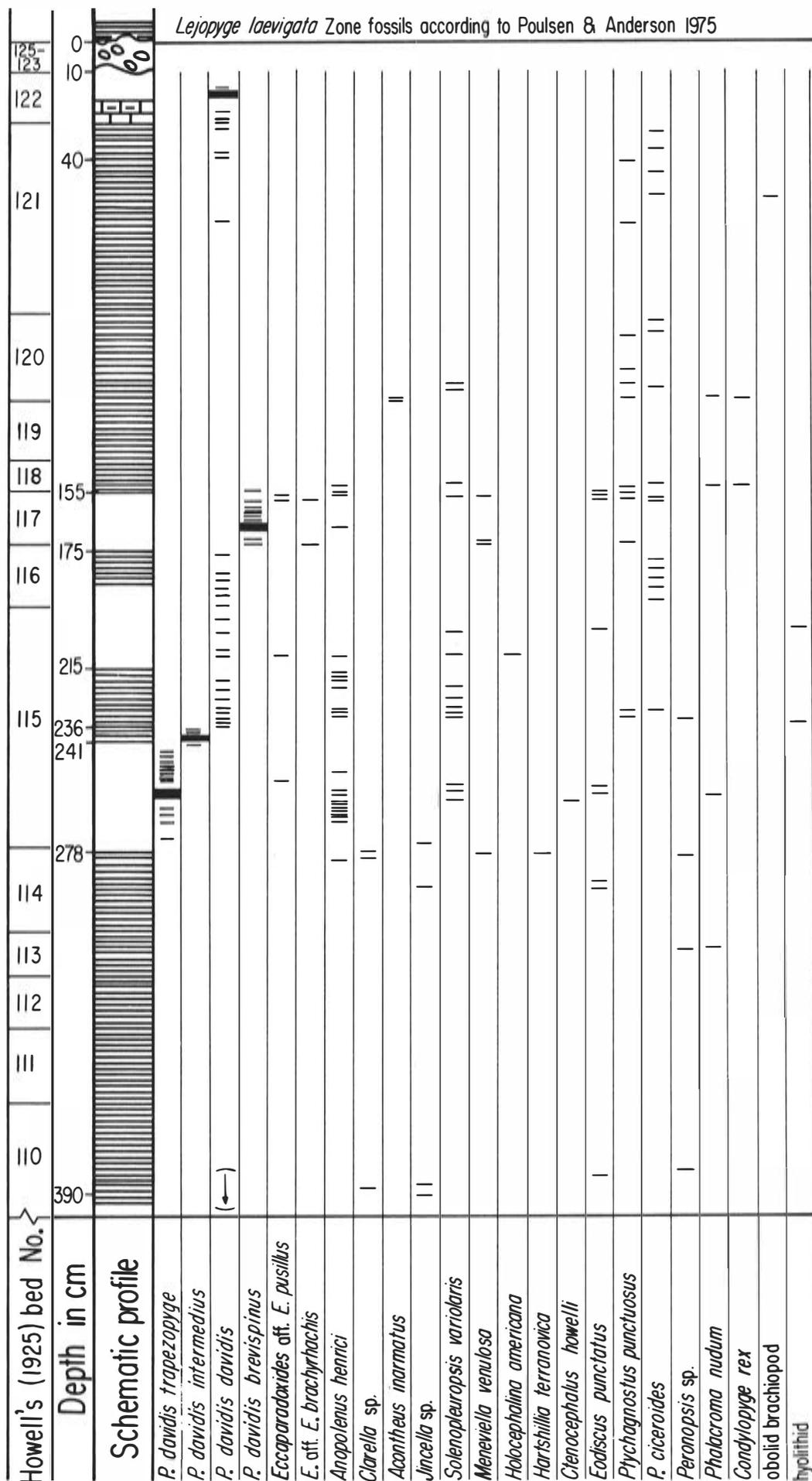


Fig. 1. Diagram showing the distribution of fossils in the studied section of *Paradoxides davidis* beds on the east side of Manuels River, Southeastern Newfoundland. The sequence consists of grey to black unevenly cleaved silty shales (white areas) and harder, fissile silty shales (shaded areas) occasionally pyritiferous and thin bedded. Depths are measured with reference to the top of a phosphatic conglomerate layer (HOWELL's bed No. 125) which is irregularly bedded and signals the upper end of the *Paradoxides davidis* range. Each mark represents the occurrence of one or several specimens at that approximate depth. Complete exuvia were found in four occurrences, indicated by solid black areas.

It proved difficult to correlate exactly with HOWELL'S measured section, although the field distance between the two sections is only about 100 m. This difficulty may be caused by slight differences in the lithology and thickness of beds as well as by differences in weathering and observation techniques. On the whole, however, there is no doubt that the two sections correspond rather closely.

We have taken as reference level the phosphatic conglomerate at the top of the *P. davidis* beds. This characteristic layer, which was described by HOWELL (1925) as a 5–15 cm (2–6 inches) thick »shale« with phosphatic nodules and referred to as bed 125, is equally developed on the east side of the Manuels River. Its stratigraphic significance was recently discussed by POULSEN & ANDERSON (1975) in contrast with previous interpretations by WALTERS (1900), HOWELL (1925) and HUTCHINSON (1962). It is regarded as marking a break in sedimentation within the upper part of the Middle Cambrian sequence and in view of its widespread geographic occurrence it represents a convenient reference standard. The section measured comprises 396 cm from the top of the phosphatic conglomerate. Further down the section is covered by talus. The faunal list and stratigraphic succession are given in Fig. 1. A detailed description of the lithology of the sediments is presented in the next section. In ascending order, no determinable form of *Paradoxides davidis* was encountered for roughly the first 130 cm of the measured section. The next 25 cm (278–241 cm in the vertical column of Fig. 1) are characterized by the exclusive occurrence of a wide-tailed form of *P. davidis* distinguished here as a new subspecies *P. d. trapezopyge*. A level in the middle part of this sequence is particularly rich in almost complete exuviae. Above the top of the range of *P. d. trapezopyge* the standard narrowtailed *P. davidis*, distinguished here as the subspecies *P. d. davidis*, occurs at 236–175 cm. A thin bed (241–236 cm) between the ranges of these two subspecies yields a form having pygidium of intermediate morphology between *P. d. trapezopyge* and *P. d. davidis*. This intermediate form is distinguished as *P. d. intermedius*. At the 175 cm level, *P. d. davidis* is replaced by another new subspecies, the slender and coarsely granulose *P. d. brevispinus*. Above this layer, the fauna becomes very sparse in a sequence of dark pyritiferous and manganese shales, in general very thin bedded and containing occasional fragments of *P. davidis*, subspecies unidentified. Seemingly typical *P. d. davidis* reappears once more 40 cm below the top of the section. No paradoxidids are found in the uppermost 10 cm. Part of these fossiliferous strata (HOWELL'S bed 122) is thick bedded and characteristically distorted by compression from large lenses of the overlying phosphatic conglomerate. To determine whether *P. d. trapezopyge* is the oldest subspecies of *P. davidis* at Manuels, we examined HOWELL'S section on the west side of the river, exposed over most of its thickness. We found this exposure considerably more weathered, water-logged and limy than on the east side. We were able however to locate a shale bed containing exuviae of *P. d. trapezopyge*, of thickness, comparable to that on the east bank exposure, most likely corresponding to the lower part of HOWELL'S bed 115. About 480 cm below this level we could identify a layer (720–750 cm depth using the scale established for the east bank) with abundant thoracic sections and pygidia of *P. d. davidis*. Thus the occurrence of the new subspecies of *P. davidis* seems restricted to a relatively narrow band of younger strata within HOWELL'S *P. davidis* zone.

Recently, POULSEN & ANDERSON (1975) reported findings of *Paradoxides* sp. above the phosphatic conglomerate defining the upper limit of the sequence investigated here. This fauna contains larval stages, in contrast with the underlying *P. davidis* beds where only holaspides are found. Two small cranidia (POULSEN & ANDERSON 1975, Pl. 1, Figs. 4, 6) show fairly distinct S3 and S4 anterior glabellar furrows and could represent *P. forchhammeri*.

Although these authors discuss this possibility, they refrain from considering this assignment as established. Indeed, as will become apparent from the present study, the presence of the two pairs of interrupted S3 and S4 in these specimens favours this attractive interpretation in contrast with an assignment to one of the subspecies of *P. davidis*.

Lithology of the sediments and environmental-faunal correlation.

The depositional structure and mineralogy of the shales in the measured section (at selected depths) on the east side of the Manuels River and at one particular depth on the west bank exposure, have been examined in some detail. Purpose of this study was to search for possible correlations between the observed faunal changes and lithological variations, which in turn could be related to variations in the environmental conditions at the time of deposition of the sediments. Furthermore this study may provide useful clues toward environmental reconstruction and account for some of the unusual features of preservation of the fossils to be described in the following.

A semi-quantitative determination of the principal groups of clay minerals was obtained from powder x-ray diffraction analysis, following the basic procedures outlined by e. g. BRINDLEY (in BROWN (1961)). In particular, a binary mixture of 50% quartz and 50% 2M₁, muscovite, prepared like the shale samples, was used as the main standard. (2M₁, muscovite was found to approach best the spectral structure observed in the shale samples). The samples of shale were crushed and sieved through a 200 mesh (grain size ~ 70 µm or less), and diffraction spectra obtained with a Cu K_α radiation x-ray diffractometer. Quartz is the dominant fraction throughout the studied sequence (see table 1), next in abundance are clay minerals of the illite group (essentially of muscovite type), and the chlorites (inclusive of minerals of the 7 Å group such as chamosite). A breakdown of the mineral fractions obtained at various levels is given in Table I. These results are not inconsistent with data reviewed by PETTIJOHN (1975) relating to the mineral composition of shales, and in particular with the data of SHAW and WEAVER (1965) for Paleozoic shales. We note consistently high quartz fractions, possibly indicating a substantial silt content. In two occurrences, both represented by black shales, does the mineral composition exhibit some distinctive character. At the top of the sequence (10–40 cm), the chlorite fraction is significantly higher than average. This black shale is hard and fissile. The lowermost level examined (720–750 cm) on the contrary, is essentially devoid of chlorite or 7 Å minerals but may contain a small fraction of vermiculite (dominant 14 Å region reflection). This shale also contains a significant fraction of finely dispersed pyrite, it is extremely brittle and cleaves into paper thin flakes. The characters of this shale in particular suggest that a substantial amount of organic matter must have been originally present in the sediments. This may have been partly replaced by pyrite. A carbonaceous residue can be collected after digestion of the shale in HCl and HF. For comparison, data obtained for the black shale of the Menevian beds at Porth-y-Rhaw, Wales, are also shown in Table I. This is characterized by an unusually high chlorite fraction, much as for the uppermost level of the *P. davidis* beds at Manuels, accompanied however by less mica and more quartz.

Further insight is provided by a study of the vertical profile from polished sections of the strata, when photographed while immersed in xylene. This method enhances color variations to the point of revealing structure even in apparently solid black sections. Photographs of sections corresponding to the selected levels of Table 1 are shown in Plate 1, Fig. 1–10 (Manuels) and Plate 2, Fig. 4. (Wales). Only for the extremely fissile black shale at the

Depth in Section (cm) a)	Depth of sample subunit(cm)	Chlorite Chamosite	Illite b)	Quartz	Pyrite	Calcite	Fissility	Color	Lamination	Dominant <i>Paradoxides</i> members
10–40	16–20	0.26 c)	0.30	0.43	–	–	blocky	black very thin	parallel,	<i>P. davidis davidis</i>
155–175	165–170	0.13	0.37	0.49	–	–	uneven d)	gray-greenish to black	banded, graded	<i>P. davidis brevispinus</i>
215–236	224–229	0.15	0.25	0.55	–	0.04	slabby	gray lenticular	irregular,	<i>P. davidis davidis</i>
236–241	239–241	0.12	0.35	0.53	–	–	slabby black	gray-	average	<i>P. davidis intermedius</i>
241–278	255–261	0.14	0.35	0.55	–	–	slabby greenish to black	gray-graded	banded,	<i>P. davidis trapezopyge</i>
241–278	263–268	0.10	0.33	0.57	–	– cleavage	conchoidal	gray	} thick	
720–750 e)	730–733	0.06 f)	0.38	0.49	0.08	–	papery	very black very thin	parallel	<i>P. davidis davidis</i>
Wales g)	0.34 c)	0.13	0.57	–	–	blocky	black	uneven non-parallel		<i>P. davidis davidis</i>

Table I. Mineral fractions from powder x-ray diffraction analysis and general characters of the shale.

a) The fractions given refer to individual samples obtained by filing vertical sections of strata typically 2–5 cm thick. Such sections were in turn obtained from those slabs of shale which contained several fossiliferous laminae. Thus the fractions represent the average composition of the fossil-bearing subunits of the quoted intervals. b) Essentially 2 M1 Muscovite. c) Mostly chlorite. d) From thin, parallel cleavage, to conchoidal fracture massive cleavage. e) Exposure on West bank of Manuels River. f) Possibly vermiculite. g) Specimen of the Menevian beds, unspecified depth, Porth-y-Rhaw.

720–750 level, a stable section could not be obtained. Abbreviated comments in Table 1 summarize the character of the sediments. In general the texture of the shale is extremely fine for all Manuels samples, in contrast with a coarser texture for the sample from Wales. Photographs at 2 x (left hand side of Plate 1) convey some feeling for the lateral extent of the structure, while details at 5 x (right hand side) enable individual laminations as thin as 20 μ m to be resolved. Extremely thin, parallel and extended laminations are observed in the black shale at the 10–40 cm level. This suggests a low rate of sedimentation in a very tranquil environment. At two levels, 155–175 cm and 241–278 cm respectively, a characteristic banded pattern is observed. This results from the alternation of light and dark layers in general a few millimeter thick. Since the mineral composition of light and dark laminae is essentially the same (see the two samples at 241–278 cm in Table 1), the difference in color must be attributed most likely to the presence of different amounts of organic material. Clay and silt particles were thoroughly mixed throughout. The pattern suggests in several instances, rhythmic deposition. Some of the beds are graded and could be described as microturbidites. Deviation from regular parallel laminations is generally due to the presence of deposited fossil remains. The layer at 215–236 cm depth differs in several respects from any of the other. Here the lamination seems to have been at times obliterated by bioturbation, lenticular bedding is occasionally present and layers of accumulation of transported fossil remains are evident. This is the only shale where a small amount of calcite was detected by x-ray analysis, clearly contributed by calcified trilobite exoskeletons. Relevant to the conclusion which may be derived from the above

is the observation that substantially identical detailed vertical profile of the strata and faunal characteristics have been recently ascertained in a quarry exposure at Kellygrews, separated from the Manuels section by a field distance of 6.25 km.

It is tempting to correlate the above lithological information to gain some insight concerning at least some aspect of the depositional environment. Of particular interest are the variations in such environment, which in turn could be correlated with the most significant faunal changes which have been observed throughout the sequence. The occurrence of black shales is usually interpreted in terms of anaerobic, strongly reducing depositional environment (see e. g. PETTIJOHN, 1975: 284). This may appear either in deep dense stagnant waters or more generally in bodies of water which may have become isolated. In the measured part of our sequence there are two occurrences of black shale, one at the 10–40 cm bed, the other at the 720–750 cm bed. In both cases the evidence of extremely quiet deposition and low sedimentation rate suggests a stagnant environment. However this may not have been identical in the two cases. For the lower occurrence, known from the detailed description of these beds by HOWELL (1925) to be part of a rather extended sequence (~ 5 meters) of black, pyritiferous shales, the mineralogical composition, in particular the substantial amount of authigenic pyrite favor reducing conditions, perhaps at considerable water depth. For the upper occurrence, the mineral composition favors a more neutral environment. The unusually high chlorite fraction (almost double of the average content of underlying shales) of this black shale demands a special source, to be found perhaps in a transient contribution from volcanoclastic debris. In this case

there is independent evidence (POULSEN and ANDERSON, 1975), that the shale in question, just underlying the conglomerate layer taken as reference, was deposited during a widespread temporary regression due to tectonic activity, marking the end of the *P. davidis* zone at Manuels and other localities. This makes it plausible then that the 10–40 cm bed may have been built in an isolated or semi-isolated body of water, not necessarily very deep.

In contrast, the shales in the middle portion of the measured section, from 155 to 278 cm, suggest a different depositional scenario. The characters of two beds, at 155–175 cm and 241–278 cm respectively, still suggest deposition well below the wave base, but with a more dynamic input of sedimentary material. Periods of slow sedimentation are suggested by the dark laminae, rich in organic matter, but the lighter laminae, generally graded, indicate sudden events of turbidite-type deposition of finely particulate and thoroughly mixed clay and silt. This picture, and the observation that the same vertical profile extends over a tract of several kilometers is suggestive of a rather deep basin or shelf, possibly opened to extended turbidity currents. A still different picture must be drawn for the bed at 215–236 cm. Here the characters revealed by the vertical profile and the presence of calcite, most likely of biochemical origin, suggest a more turbulent, aerated environment, either warmer or more alkaline than for the other sediments.

Although the above rudimentary environmental reconstructions may be questioned in favor of alternative interpretations, we wish to focus on the evidence that some changes have indeed occurred at several instances throughout the sequence. The last column in Table 1 indicates the identified subspecies of *Paradoxides davidis* for the beds discussed above. Although the same subspecies, *P. davidis davidis*, does occur in strata of different lithology and thus possibly in different habitats it does appear that a definite correlation exists between changes in the lithological facies and faunal replacements. Such correlation, to be taken up in a later discussion, will pave the way to find plausible interpretations for the complex pattern of alternating phenotypic variation which have been observed.

General characters of the fossil fauna.

As can be appreciated from Fig. 1, the frequency of occurrence of trilobite remains in the section studied, is subject to extreme variation for different strata. Most fossiliferous beds contain separated (but not broken) exoskeletal parts, suggesting a tranquil depositional environment consistently with the conclusion of the previous section. There are a few exceptional thin beds where complete exuviae of large *Paradoxides davidis* are numerous and well preserved. One of these contains exclusively the subspecies *P. d. trapezopyge*, with individuals averaging 20–30 cm in length, which are densely distributed on the surface of the bedding plane, still without overlapping each other. Such complete exuviae are predominantly found ventral side down and randomly oriented, a feature which once again suggests a quiet deposition. In general even complete specimens represent exuviae. The molting process seems to have occurred as a result of the complete release of the cephalic sutures. Often the exoskeletal elements of the cephalon are found only slightly displaced from their life-position, at times the free cheeks are overturned (see e. g. Pl. 7:2). On occasion molting did occur even if not all sutures were released. The features of exceptional bedding planes such as the one just described for *P. d. trapezopyge* suggest they may represent an undisturbed molting environment, much as described by HENNINGSMOEN (1975). A similar situation is encountered for *P. d. brevispinus*. At least for the subspecies of *P. davidis* no larvae of protaspis or meraspis degree have been identified in the section of Fig. 1. Even small holaspides are missing,

the shortest pygidium found extrapolating to a body length, excluding spines, of about 8 cm. The distribution of pygidial lengths for different stratigraphical intervals in the sequence is shown in Fig. 2. Fragments of the largest specimens occur within a (relatively) narrow interval (215–236 cm). The other intervals show a limited variation in individual size, much smaller than the full breadth of the size range of holaspides. On the other hand, small trilobites such as agnostids, eodiscids and *Solenopleuropsis*, are plentiful concurrently with the population of adult *P. davidis*. This suggests that the absence of small *P. davidis* exuviae is not to be attributed to size sorting, but that the habitats for different size groups of the latter may have been different. Aside from the occurrence of large adults of *P. davidis davidis* at one particular level, noted in Fig. 2, we note that the size distribution for *P. davidis trapezopyge* is shifted toward somewhat larger sizes than those of *P. davidis davidis*.

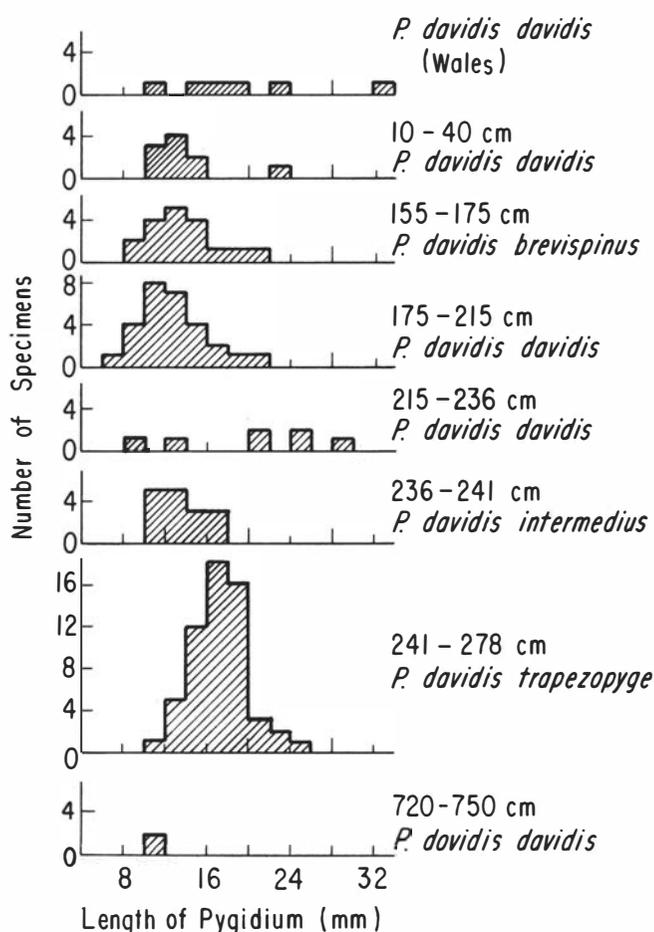


Fig. 2. Size distribution of *Paradoxides davidis* at different levels in the Manuels section (see also Figs. 1 and 9) as represented by the pygidial length. The size range at each level does not cover the full range of sizes for the species. As seen from the distributions for *P. d. davidis* which cover different size ranges, the size concentration is not a characteristic of the subspecies but rather of the distinct stratigraphic levels.

The condition of preservation of the fossils in the section of Fig. 1 is generally good. The large exoskeletons are compressed to about 1/3–1/4 of their original relief as seen from a comparison with uncompressed specimens from Europe, preserved in limestone. The integument is occasionally calcitic as in the 215–236 cm bed, generally however replaced by limonite, with usually bright yellow (to deep red ochre) surfaces. Large cavities such as that between the glabella and rostro-labral plate of *P. davidis* are

occasionally found unfilled. There is no distortion due to tectonic shear. Aside from compressional flattening and deformation, the trilobites in the beds 10–40 cm below the top of the phosphatic conglomerate are affected by a peculiar wrinkling of the exoskeletal surface which, unless recognized as a general disturbance, can simulate extravagant ornamentation.

Systematic description

Paradoxides davidis SALTER, 1863

- 1863 *Paradoxides davidis* SALTER; p. 275, text-fig.
 1864 *Paradoxides davidis* SALTER; p. 234, Pl. 13: 1–3.
 1902 *Paradoxides davidis* SALTER; GRONWALL, p. 106, P. 2: 3–7.
 1935 *Paradoxides davidis* SALTER; LAKE, p. 203–208, Pl. 27: 1–2; 28: 1–3; 29: 1–3.
 1952 *Paradoxides davidis* SALTER; HUTCHINSON, p. 76–77, Pl. 2: 6–8.
 1962 *Paradoxides davidis* SALTER; HUTCHINSON, p. 115, Pls. 19: 10, 20, 21, 22.
 1972 *Paradoxides davidis* SALTER; FLETCHER, p. 92–93, Pl. 49: 11; 50: 1–6; 51: 1–2.
 1975 *Paradoxides forchhammeri* ANGELIN; (preliminary identification) LEVI-SETTI, p. 189–190, Pls. A3 – A7.
 1975 *Paradoxides davidis* SALTER; LEVI-SETTI, p. 190, Pls. A8 – A10.

General considerations

Although *P. davidis* has been mainly described from distorted or fragmented material, we have a fairly good idea of its morphology from the literature. It has been reported from Britain, South Scandinavia, Nova Scotia, Newfoundland, and with some uncertainty from Spain.

P. davidis is a typical member of *Paradoxides*. This means that the labral plate (hypostome) and rostral plate are fused into a rostro-labral plate, in contrast with the known condition in the species of *Eccaparadoxides* and *Hydrocephalus*. It differs from

other species of *Paradoxides* except *P. forchhammeri* in having a slightly indented and arched posterior margin of the pygidium. The pygidium is commonly narrow and fused with the last thoracic tergite. *P. davidis* differs from *P. forchhammeri* in having a weaker ornamentation and in the absence of the glabellar furrows S3 and S4, which are well developed in the latter.

LAKE (1935: 207 and Pl. 28: 3) states that the number of thoracic segments is always 19. He erroneously thought that the last thoracic tergite is always fused with the pygidium and consequently counted it as part of the pygidium. However, the last thoracic tergite always preserves its »thoracic« appearance, and as seen from specimens from Bornholm and Newfoundland it is not always fused with the pygidium. It is therefore preferable to count it with the thorax, which, therefore, contains 20 segments as a rule.

The *Paradoxides davidis* material collected at Manuels River contains evidence of infraspecific phenotypic variation, distinctly associated with stratigraphic position, as well as a range of individual variation. Subject to such variations are several characters among those usually referred to in distinguishing species of paradoxidaceans.

We are led to recognize at least three different subspecies of *P. davidis*, on the basis of the morphology of the pygidium and stratigraphic occurrence. One form (*P. d. trapezopyge*) differs from the original type (*P. d. davidis*) with rectangular or tapering pygidium, by showing a posteriorly expanding trapezoidal pygidium, which necessarily forces the last thoracic spines to differ from those in the typical form. Many almost complete specimens were collected of the wide-tailed variant, which is the best known of the forms discussed. The morphological gap between *P. d. davidis* and *P. d. trapezopyge* is bridged by an intermediate form, *P. d. intermedius*. The distinction between the three subspecies is illustrated in Fig. 3, where the anterior width W_1 of the pygidium is plotted against the posterior width W_2 for some 41 pygidia of *P. d. davidis*, 58 pygidia of *P. d. trapezopyge* and 16 of *P. d. intermedius*. For the latter two subspecies the only criterion used in distinguishing the representative points in Fig. 3 by different symbols, was their stratigraphic position. This correlation is further illustrated in Fig. 4a and b. Here plots of the ratio W_2/W_1 are shown for the various beds sampled (Fig. 4b) and the corresponding average values and their standard deviations plotted in Fig. 4a versus stratigraphic depth. As can be seen, the samples at 241–278 cm and 236–241 cm differ significantly from those associated with *P. d. davidis*. While the morphological details will be further illustrated in the systematic description of the various subspecies, both Fig. 3 and Fig. 4 contain the basic evidence for a distinction between different phenotypes. In fact, it becomes compelling to describe the subspecies themselves on the basis of the biometric parameter W_2/W_1 .

Another distinct form (*P. d. brevispinus*), occurring exclusively at a depth of 155–175 cm, has pygidium essentially like the nominate form, but very short pleural spines, which confer to the trilobite a particularly slender and tapered overall shape.

The intraspecific character of such phenotypic variations, which do not affect in any way e.g. the cranial morphology, is substantiated by the plot of Fig. 5, showing that the morphology of the labral plate is essentially identical for the various phenotypes. In addition to variation characterizing distinct subspecies, random individual variability is also found in characters such as the number of thoracic segments and the articulation of the pygidium. The variability in the number of thoracic segments is illustrated in Fig. 6 for the various subspecies of *P. davidis*. In *P. d. davidis* and *P. d. trapezopyge*, most individuals have 20 tergites, and only a few exceptional specimens have 19 or 18 tergites. In *P. d. brevispinus* however 20 and 21 tergites are almost equally frequent. The pygidium may be occasionally articulated, but in most cases it is fused with the last thoracic tergite. The fusion

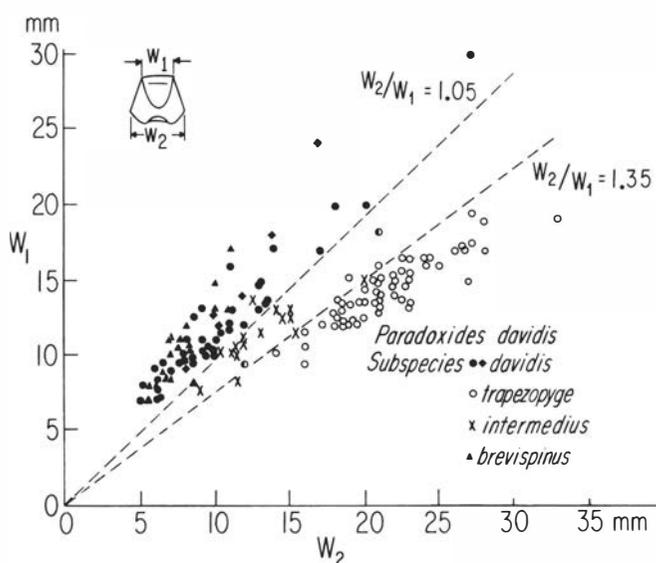
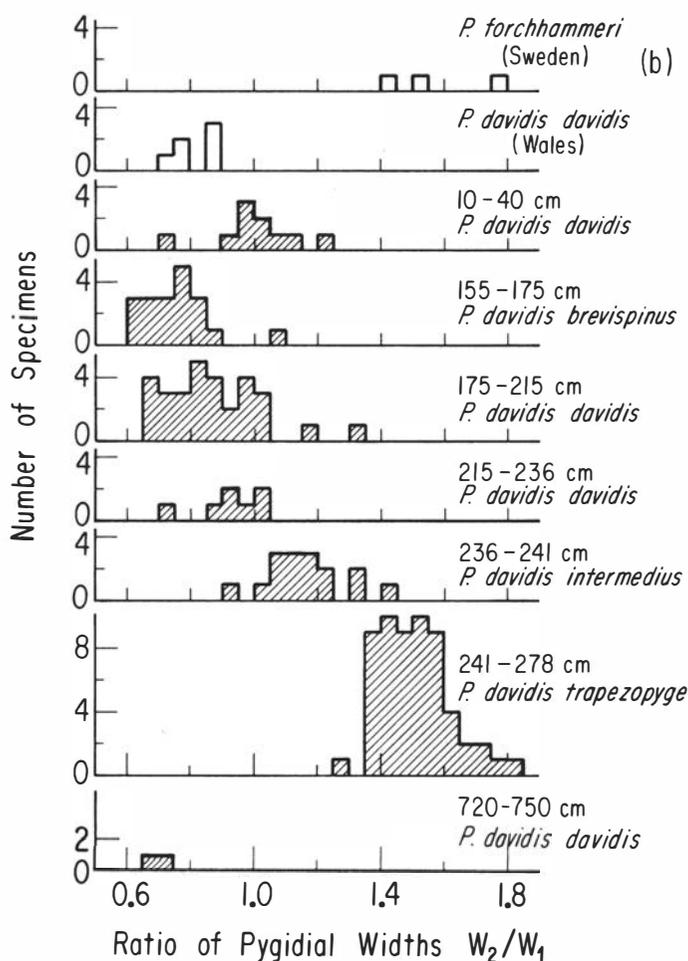
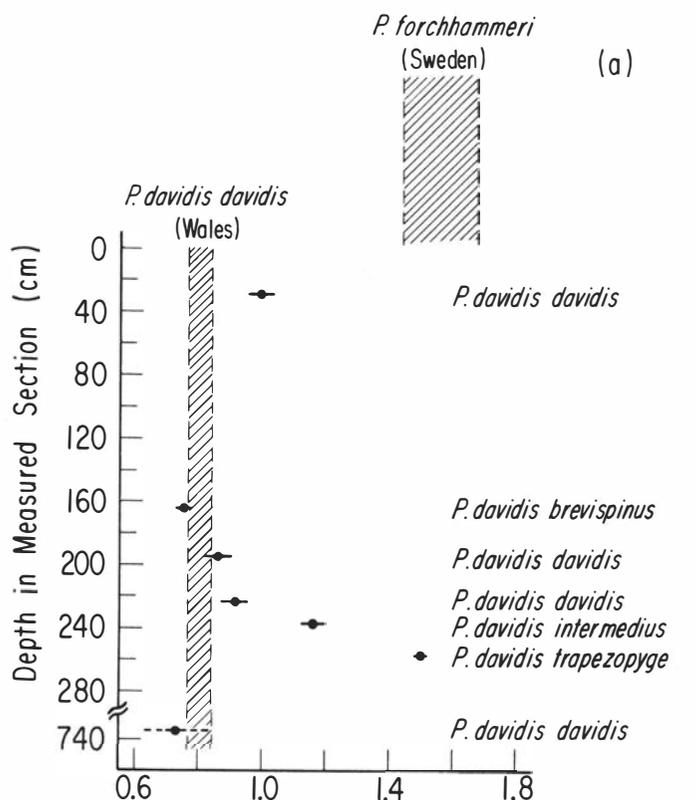


Fig. 3. Plot of anterior versus posterior pygidial widths showing the separation of the different subspecies of *Paradoxides davidis* with regard to pygidial morphology. Growth is linear in all cases, the slope and intercept of the regression lines (as can be appreciated by visual interpolation), differ substantially for *P. d. davidis* and *P. d. trapezopyge*. Separation of *P. d. intermedius* from these two components is based on its stratigraphic position, at the interface between the ranges respectively of *P. d. trapezopyge* and *P. d. davidis*.



may be only axial, or it may extend laterally to the pleural field. No correlation has been noticed between any particular mode of fusion and any particular subspecies.

***Paradoxides davidis davidis* SALTER, 1863.**

Pl. 2 Fig. 1-3, Pl. 3 Fig. 1-5, Pl. 4 Fig. 1-11, Pl. 5 Fig. 1-11.

D i a g n o s i s : Subspecies of *P. davidis* with a mean pygidial width ratio W_2/W_1 ranging from about 0.70 to 1.05.

H o l o t y p e : BM I 1. Menevian beds at Porth-y-rhaw, St. Davids, S. Wales. Pl. 2 Fig. 1.

R e m a r k s : We characterize as the nominate subspecies the form described from the type locality at Porth-y-rhaw, St. Davids, Pembrokeshire and known from many other localities in Britain, Scandinavia and eastern North America. At Manuels this form has a discontinuous vertical distribution (cf. Fig. 1). For purposes of comparison with the material from Manuels, Plates 2 and 3 contain photographs of specimens of this subspecies from Porth-y-rhaw. With the exception of Pl. 2 Fig. 1, portraying a cast of specimen at the British Museum (BM I1), all other specimens were collected and loaned by E. N. K. Clarkson, and are deposited at the Grant Institute of Geology, Edinburgh.

The abundant exuvial remains which were collected in the measured sequence at Manuels provide a detailed comparison with the material from the British type locality. Relevant specimens are illustrated in Plates 4 and 5. This comparison confirms the previous identification provided by WALCOTT (1900), HOWELL (1925), HUTCHINSON (1926) and FLETCHER (1972). The identity of the form from Manuels with the corresponding British trilobite acquires particular significance in this context however. Since different subspecies are identified at Manuels, it is important to establish whether the same subspecies are indeed present at both localities. It appears that only *P. d. davidis* is represented at the British locality. There is little doubt that the British and Newfoundland *P. d. davidis* are indeed the same trilobite.

The condition of preservation of the Manuels material is generally superior to that of the British specimens, which are commonly distorted by tectonic shear. For this reason and to better visualize the difference between the various subspecies of *P. davidis*, a reconstruction of *P. davidis davidis* is presented in Fig. 7a.

Fig. 4.a. - Mean values and standard deviations of the mean for the ratio of pygidial widths W_2/W_1 plotted as a function of median stratigraphic depth in the Manuels section, for the depth intervals of Fig. 4 b. For comparison, the ranges of the mean of W_2/W_1 (within \pm one standard deviation) for *Paradoxides davidis davidis* from Wales and *Paradoxides forchhammeri* from Sweden are also indicated. Only two pygidia are available from the 720-750 cm level on the west bank of the Manuels River. In view of this insufficient statistics, the error on the mean value of W_2/W_1 for this depth (dashed) was estimated assuming a sample stand. dev. similar to that of the other distributions. The assignment of this faunal member to *P. davidis davidis* is however well established.

b. -Distributions of the ratio W_2/W_1 for samples of *Paradoxides* collected at various stratigraphic depths in the Manuels section, for *P. davidis davidis* from Porth-y-rhaw, Wales and *P. forchhammeri* of Sweden.

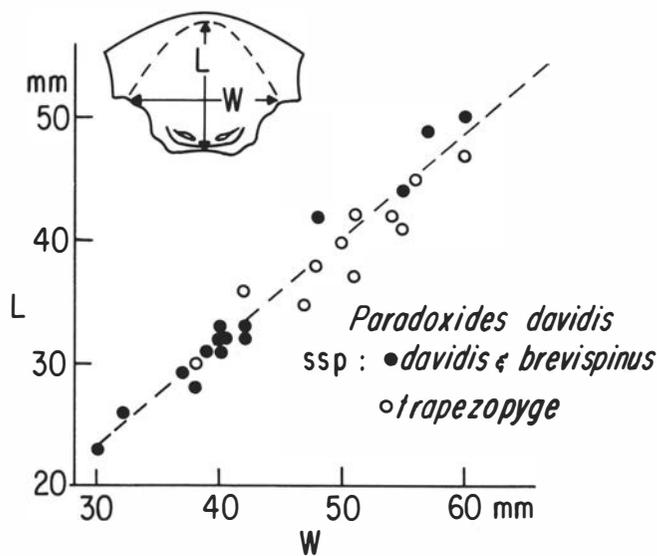


Fig. 5. Plot of length versus width of the labral component of the rostro-labral plates for different subspecies of *Paradoxides davidis*. All points are consistent with a common growth line, reflecting in this case identical morphology.

Description: As mentioned in the previous section the morphological characters which are subject to variation between subspecies refer to the shape of the pygidium and of the pleural spines. In *P. d. davidis*, the pygidium is parallel sided to distally tapering, as illustrated quantitatively in Fig. 3 and 4. The following mean ratios have been calculated (sample stand. dev. in brackets): 10–40 cm, 10 specimens, 0.99 (0.13); 175–215 cm, 30 specimens, 0.87 (0.15); 215–236 cm, 7 specimens, 0.91 (0.11). Two specimens from the 720–750 cm bed have ratios 0.69 and 0.76 respectively.

The pygidial rhachis contains one distinct axial ring and faint traces of two or three additional segments. It is commonly terminated by a crescentic boss. The posterior margin is slightly indented and convex, arching upwards. The largest pygidium found is shown in Pl. 4, Fig. 1. The right lateral border of the pygidium in this example bears evidence of the merging of tergites which led to the formation of a pygidial shield. In fact such border is shaped much as a diminutive posterior pleural spine, attached to the only well defined axial ring of the pygidium. From the known proportions of the body for this species, one can infer that the overall length of the rhachis was, for this individual, about 37 cm, much as the size of BM 11 shown in Pl. 2, Fig. 1. The pleural spines are generally falcate and are progressively longer and swept backwards toward the posterior part of the thorax. This progression culminates in the exaggerated and characteristic saber-shaped last pair of spines, projecting backwards for a length about five times that of the pygidium (measured excluding the articulating half-ring). These spines converge at about half length and then diverge again; in the distal region their cross section is circular. (Including the last pair of spines, the overall estimated length of the largest individual discussed above becomes about 48 cm). The second from the last pair of pleurae (basal portion plus spine) may reach up to four times the length of the pygidium. The last thoracic tergite, carrying the extraordinarily long pleural spines, may either articulate freely with the pygidium or be fused axially and in most cases also laterally to the latter. Lateral fusion with the pygidium may represent a functional character, serving to reinforce and constrain the long spines in their characteristic posture.

Other morphological characters of the species will be discussed in connection with the description of *P. d. trapezopyge*, in the next section.

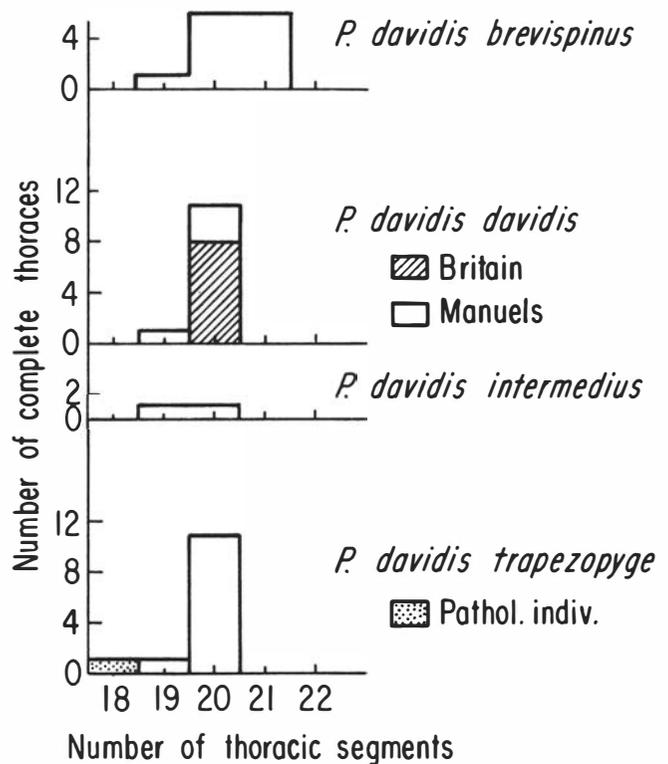


Fig. 6. Distribution of the number of thoracic segments for different subspecies of *Paradoxides davidis* SALTER. A total of 39 complete holaspid thoraces are represented. The number of tergites is variable even within the same subspecies, most remarkably in *P. d. brevispinus*, where 20 and 21 tergites are almost equally represented.

Paradoxides davidis trapezopyge, new subspecies.

Pl. 6 Fig. 8, Pl. 7 Fig. 1–5, Pl. 8 Fig. 1, 3, 4, 7, 8, Pl. 9 Fig. 1–3.

Diagnosis: Subspecies of *P. davidis* with a mean pygidial width ratio W_2/W_1 above 1.35.

Holotype: FMNH PE 25013, Pl. 7, Fig. 2.

Locus typicus: Section depth 241–278 cm below top of phosphatic conglomerate marking the end of the *P. davidis* range. East bank of Manuels River, Manuels, Newfoundland.

Remarks: We attribute to this subspecies a specimen previously figured as *Paradoxides davidis* SALTER by HUTCHINSON (1962, Pl. XXI) who did not notice any distinctive characters; indeed he stated (p. 115) that »the Newfoundland specimens agree in all respects with those from England«. We also substitute this identification in lieu of the preliminary identification as *Paradoxides forchhammeri* ANGELIN for the specimens already figured by LEVI-SETTI (LEVI-SETTI, 1975, Pl. A3, A4, A5, A6, A7). One of the latter (Pl. A5) is also reproduced here in Pl. 6, Fig. 8. Another almost complete individual is shown in Pl. 7, Fig. 2, and Plate 8 illustrates details of the morphology of this trilobite. A reconstruction of the subspecies is shown in Fig. 7b, where it is compared with that of *P. davidis davidis* (Fig. 7a). This reconstruction, and the description to follow, are based on some 12 essentially complete exuviae of adult individuals and a substantial sample of fragments, collected at Manuels River in 1974–1977.

The basic morphological character which distinguishes *P. d. trapezopyge* from *P. d. davidis* consists in the shape of the pygidium. In the former, as the name implies, the pygidium is expanded backwards to acquire a trapezoidal shape, in contrast with the subrectangular or tapered outline of the latter. This distinction is quantitatively illustrated in Fig. 3 and 4.

The mean W_2/W_1 ratio calculated from 58 pygidia is 1.50, with sample stand. dev. 0.10. As already mentioned, aside from the last pair of pleural spines, discussed below, there seem to be no other primary characters of distinction between *P. d. trapezopyge* and *P. d. davidis*. Most of the detailed description to follow then, aside from a few distinctive primary and derived characters of the form, will parallel the description of *P. davidis* SALTER at the species level.

Description: The cephalon is roughly semicircular, with long genal spines and a very bluntly pointed anterior end. The glabella is delineated by forward diverging dorsal furrows, which appear to have been straight before compressional deformation.

The occipital and two posterior glabellar furrows are well developed and traverse the glabella completely. There is commonly no trace of additional glabellar furrows. The course of the glabellar furrows exhibits a fair degree of variation, but much of this is clearly caused by post-mortem deformation. The anterior and lateral parts of the frontal lobe are ornamented with concentrically arranged terrace lines, which become short and discontinuous laterally. The rest of the glabella has a fine uniform granulation, evident particularly in external impressions. The occipital ring carries a small median node about 1/3 of the width from its posterior margin. The frontal margin is quite narrow, about half as wide as the posterior border of the fixed cheek. The latter shows an irregular granulation, considerably coarser than that of the glabella. The surface of the fixed cheek may also show an irregular undulation, which may represent a vascular prosopon. A similar but more radiating pattern can be observed on the free cheek. A coarse vascular ridge is present on the posterior border of the free cheek. The palpebral lobe is distinctly raised, with a straight inner and curved outer boundary. The posterior end of the palpebral lobe is roughly opposite the lateral end of S1, while the front end is slightly anterior to S2. Except for the absence of strongly developed S3 and S4 glabellar furrows and a weaker ornamentation in *P. davidis trapezopyge*, the cranidium of this trilobite is remarkably similar to that of *P. forchhammeri* (see Pl. 8, Fig. 2). The free cheek has a wide and strong arched border with terrace lines which are particularly prominent on the ventral side. The genal spines are about as long as the entire glabella including the occipital lobe. The genal angle is approximately right to slightly acute. The cephalic doublure is fairly wide and provided with terrace lines throughout.

The labral plate (hypostome) is fused to the rostral plate as mentioned above. There is a pair of ridge-shaped maculae and a pair of very short blunt lateral spines. It may be remarked that the shape and ornamentation of the rostro-labral plate appear to be indistinguishable from those of *P. forchhammeri*, much as noted above for the cranidium.

In the thoracic region the width of the rhachis is approximately 5/4 of that of each pleural lobe, throughout the entire length of the thorax. The rhachis tapers gradually, to a posterior width about half the anterior width. The outline of the overall pleural region, (excluding the pleural spines) is triangular over the first 2/3 of the thorax, ovate in the last 1/3, and merges with the outline of the pleural field of the pygidium. As in *P. d. davidis*, the rhachis and the pleurae are ornamented with granules similar to those on the fixed cheek although usually less obvious and slightly smaller. This ornamentation is particularly noticeable on external impressions, as shown in Pl. 5, Fig. 11 and Pl. 8, Fig. 8. On each pleura there is one anterior and one posterior prosopic (vascular) ridge, visible in well preserved specimens. The morphology of the pleurae in *Paradoxides* differs from that of most trilobites in not exhibiting (in vertical section) a proximal horizontal hinge portion and a distal sloping pleural spine. Instead the proximal portion between the dorsal furrow and the marginal connecting device is slightly arched, with the highest portion about one third

of the distance from the rhachial furrow to the base of the pleural spines. In the absence of true hinge-lines the boundary between adjoining tergites, as seen in horizontal projection, is not a straight line but an arching line extending to a level opposite to the middle of the next anterior rhachial ring. The pleural spines appear to have been almost horizontal to slightly dipping before compression.

As in *P. d. davidis* the anterior pleural spines are short, and become progressively longer and more falcate toward the end of the thorax. The last thoracic tergite has wide, swollen pleurae adjoining the pygidium. Beyond the latter, the pleural spines taper rapidly, noticeably more so than in *P. d. davidis*. These spines typically diverge backwards, a feature which is dictated by the expanding pygidium and may be interpreted as a derived or secondary character. The total length of the last pair of pleurae is approximately four times the axial length of the pygidium. As in *P. d. davidis*, the last tergite is at times freely articulated with the pygidium, in other instances fused either only axially or along the entire contact.

The pygidium has one distinct rhachial ring succeeded by a tapering rhachis with or without faint traces of segmentation. The rhachis is generally smooth, in one instance four small dimples are symmetrically arranged along a transverse line. The lateral borders diverge backwards at an angle of about 15–20° to the axis. The postero-lateral corners are bluntly cut-off. The posterior margin is slightly indented with central part arched upward. The limit of the pygidial doublure is sometimes indicated by a ridge close to the posterior border as seen in Pl. 7, Figs. 2 and 5. The overall morphology of the pygidium is very similar to that of *P. forchhammeri*, two examples of which are shown in Pl. 8, Figs. 5 and 6. One may notice that in *P. d. trapezopyge*, the posterolateral corners confer to the pygidium, together with the posterior and lateral borders, a distinctive polygonal outline. In *P. forchhammeri* instead, the corners are rounded. Two exceptional specimens, shown respectively in Pl. 8, Fig. 4 and Pl. 9, Fig. 2, 3, do indeed approach the *P. forchhammeri* pygidial outline very closely. That the specimen shown in Pl. 9, Fig. 1–3 may represent an anomaly within the population of *P. d. trapezopyge* is suggested by a number of seemingly congenital malformations and abnormalities affecting this individual. With only 18 thoracic segments, of which the first two are fused together, this specimen has the smallest number of tergites seen for the species. Furthermore several of the pleurae exhibit atrophy or truncation and gross deformations. In addition, the pygidial rhachis shows two distinct rings, instead of a single one as the norm. In view of the pathological conditions observed, characters such as the rounded pygidial corners which may be viewed as trans-specific should be regarded with suspicion. The largest cranidium of *P. d. trapezopyge* seen measures 10.5 cm axially. This extrapolates to an overall exoskeletal length, including spines, of about 35 cm.

***Paradoxides davidis intermedius*, new subspecies.**

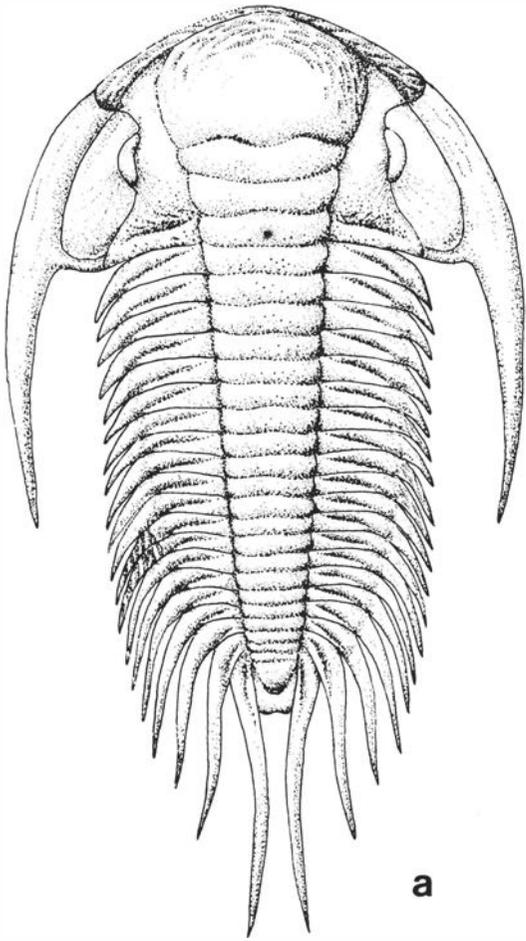
Pl. 6 Fig. 1–7.

Diagnosis: Subspecies of *P. davidis* with a mean pygidial width ratio W_2/W_1 ranging from 1.05 to 1.35.

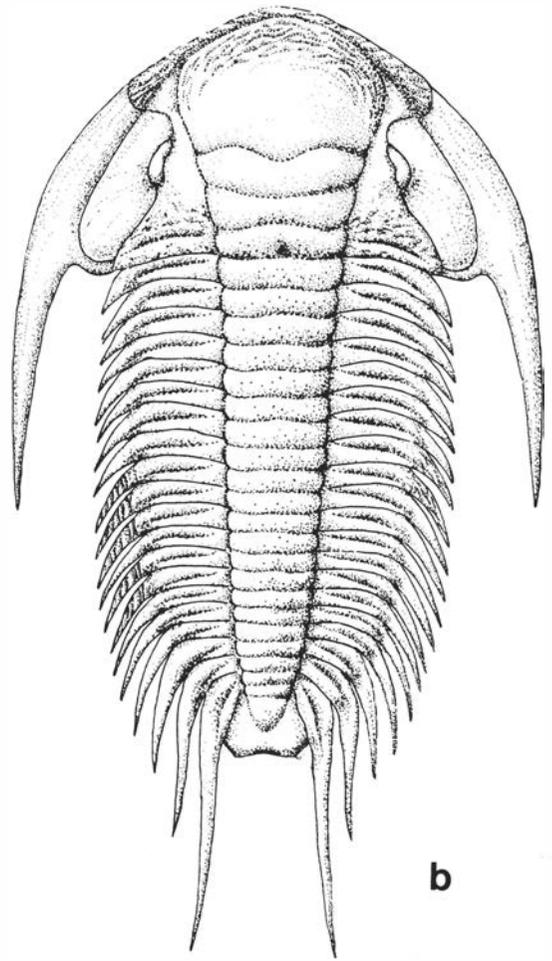
Holotype: FMNH PE 28971. Pl. 6, Fig. 3.

Locustypicus: Section depth 236–241 cm below top of phosphatic conglomerate marking end of *P. davidis* range. East bank of Manuels River, Manuels, Newfoundland.

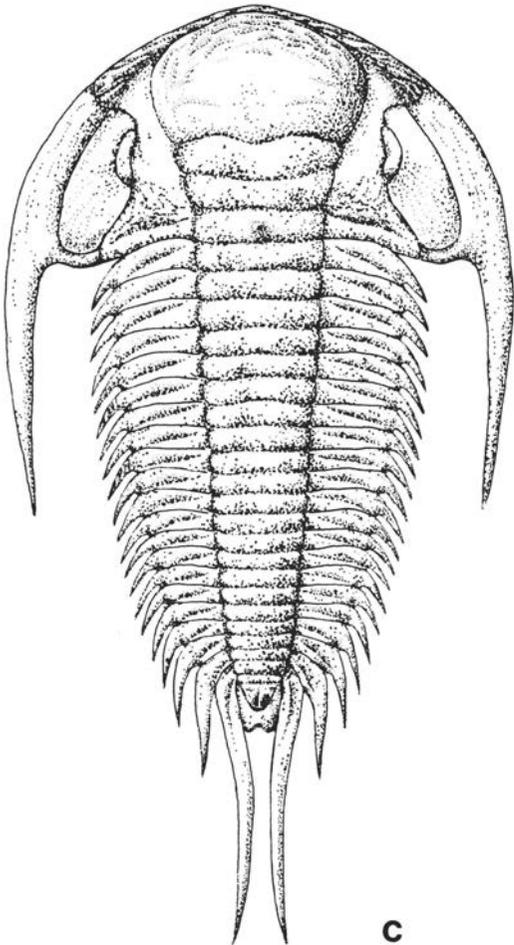
Description: Pygidia of a character intermediate between those of *P. d. trapezopyge* and *P. d. typicus* have been collected predominantly in a relatively thin layer (5 cm) located at



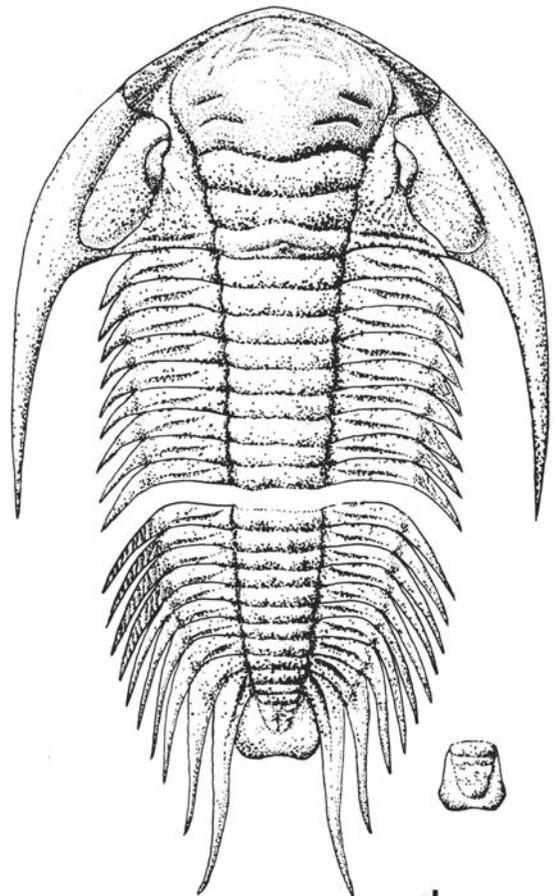
a



b



c



d

236–241 cm between the stratigraphic ranges of the two above subspecies. A few similar pygidia originate from stratigraphically higher levels, where they represent extreme variants of *P. davidis davidis*. Points indicating their widths are plotted in Fig. 3 and the ratio W_2/W_1 analyzed in Fig. 4. As implied by the location of the representative points in the plot, these pygidia expand only moderately in the posterior region, thus falling between the distributions for *P. d. davidis* and *P. d. trapezopyge*. Their overall outline is bell-shaped with truncated postero-lateral corners. The mean width ratio W_2/W_1 is 1.16 (sample st. dev. 0.13), based on 16 pygidia. To answer the question whether compression of the pygidia of *P. d. davidis* could yield pygidial shapes as observed in this case, several latex moulds of the most convex pygidia of *P. d. davidis* were flattened and the contour traced. In no case a posteriorly expanding outline could be obtained, the limiting contour being rectangular. If the pygidia of *P. d. intermedius* had occurred interspersed within the range of *P. d. trapezopyge*, one would be led to interpret their morphology as an extreme variation of individual characters. However, these pygidia occur almost exclusively at the level 236–241 cm between two well defined ranges for two distinct subspecies. From the above it seems possible to interpret their intermediate morphology as evidence of either the existence of a cline or of hybridization (secondary intergradation) between the two subspecies *P. d. trapezopyge* and *P. d. davidis*. One may also note that the last thoracic pleura and spine, as in Pl. 6, Figs. 1, 3, 6, and 7, bears intermediate characters. It tapers as rapidly as in *P. d. trapezopyge* but at variance with the latter, it converges toward the axis as in *P. d. davidis*.

A strikingly distinctive character which seems associated with both *P. d. trapezopyge* and this intermediate subspecies, is the occurrence of malformations affecting the last pair of pleurae. These may appear as short, bluntly terminated stubs as in Pl. 6, Figs. 1 and 5. Unless the result of healed injury in-vivo, such deformities may be congenital in origin. One seemingly complete thorax, part of which is shown in Pl. 6, Fig. 1, has 19 segments; another shown in Pl. 6, Fig. 3, has 20 segments.

Paradoxides davidis brevispinus, new subspecies.

Pl. 9, Fig. 5, Pl. 10, Figs. 1–7.

D i a g n o s i s : Subspecies of *P. davidis* with low mean pygidial width ratio W_2/W_1 (around 0.75) and with comparatively coarse ornamentation and notably short pleural spines.

H o l o t y p e : FMNH PE 28974. Pl. 10, Fig. 3.

L o c u s t y p i c u s : Section depth 155–175 cm below top of phosphatic conglomerate marking end of *P. davidis* range. East bank of Manuels River, Manuels, Newfoundland.

D e s c r i p t i o n : Eleven complete exuviae and fragments represent this form, distinguished from *P. d. davidis* by its exceptionally short pleural spines (aside from the last pair) and

more prominent surface ornamentation. As seen in Fig. 3 and 4 pygidia for this subspecies are, as known from 19 points, somewhat more tapered than in *P. davidis davidis*, although identical in structural details. The mean pygidial width ratio W_2/W_1 is 0.75 with a sample st. dev. of 0.10. The number of thoracic tergites is 20 or 21 with comparable frequency, as shown in Fig. 6. As in *P. d. davidis* the last thoracic pleurae are very long and converging, terminating in the characteristic saber shaped spines. The next pair of pleurae is only about half as long or less than in *P. d. davidis*, i. e. at most about twice as long as the pygidium. The difference becomes even more marked when only the length of the pleural spines is compared. For instance, in *P. d. davidis* the length of the third from the last pleural spine is about three times the length of the pygidium, but only about 2/3 of this length in *P. d. brevispinus*. The pleural spines are not only shorter than in *P. d. davidis*, but also narrower, and the posterior side of each is markedly sigmoid near the base. The shortness of the pleural spines confers to the body a distinctly tapering and slender outline (see e. g. Pl. 10, Fig. 3), whereas the thorax has a more even width in the other subspecies. The cephalon appears to be virtually identical to that of *P. d. davidis*.

The surface granulation and vascular prosopon is considerably coarser and more prominent in this subspecies than in *P. d. davidis*, *P. d. intermedius*, and *P. d. trapezopyge*, in particular in the thoracic region. This is evident in the detail of Pl. 10, Fig. 7. This character represents another example of the similarities exhibited by various subspecies of *P. davidis* with *P. forchhammeri*.

Random morphological variability and teratologies.

Random minor morphological variability is observed to affect most parts of the exoskeleton of *P. davidis*. Most notable and unprecedented among trilobites is perhaps the variability in the number of thoracic tergites, already presented in Fig. 6. The variability in this meristic quantity is necessarily quantized, the number of segments taking up values from 18 to 21. We find it remarkable that a morphological parameter previously thought as constant (for holaspides) within a trilobite species, should be subject to variation even within individual subspecies in *P. davidis*. It would seem that the onset of pygidial formation was not subject to genetic control as much as in most other trilobites. However, the variation in segment numbers is not unique; in fact a number of Cambrian trilobites show a similar variation (R. A. Robison, private communication, August 1976).

Thoracic tergite fusion, although in principle a dichotomic variable, acquires a more continuous character if the state of completion of the fusion of the last thoracic tergite to the pygidium is considered. Occasionally no fusion is present and the articulation is functional. In other cases the pygidium is fused to the thoracic rhachis, but the lateral margins are still separated from the pleurae. The fused margins of the tergites involved and the articulating half-ring may be still identifiable. Finally there are instances where the fusion is complete along the entire antero-lateral borders of the pygidium. In such cases the pygidium and last thoracic tergite may separate from the thorax as a distinct unit and this feature has caused the previous mistaken notion that *P. davidis* possessed 19 tergites (as a rule) rather than 20 as represented here.

In the pygidium, the segmentation is usually restricted to the rhachis, but occasionally a pleural furrow and marginal lobe (as in Pl. 4, Fig. 1) may be present, as vestiges of the merging of pygidial tergites. In general, only the anterior axial ring is clearly defined, however two or three additional rings may be present in some cases, separated by faint furrows or pits. Within particular subspecies, the morphological variability of the pygidium is best illustrated by the scatter of points in Fig. 3. A similar variability is

Fig. 7. Reconstruction of the principal subspecies of *Paradoxides davidis* (a, *P. d. davidis*, b, *P. d. trapezopyge*, c, *P. d. brevispinus*) and of *P. forchhammeri* (d). *P. d. brevispinus* is shown with 21 thoracic segments, the other two subspecies with 20. The outline of the thoracic region of *P. forchhammeri* is conjectural and the actual number of tergites unknown; to indicate this uncertainty, the assumed sequence of 20 tergites in the reconstruction is interrupted. The pattern of terrace lines marking the ventral side of the pleural spines and commonly exposed in exfoliated specimens, is reproduced on several pleural spines on the left hand side of the reconstructions.

encountered in the relative length of the pygidial rhachis, relief and ornamentation. The pleural spines as well show some variability, within the subspecific pattern, in length and orientation. In the cephalon, variability is observed in the curvature and course of the occipital glabellar furrows S1 and S2, partly exaggerated by compression. Furrows S3 and S4 are typically not developed in *P. davidis*, but may occasionally be traced as faint lines or very shallow furrows. The position of the occipital node is also slightly variable. In specimens thought to be moults, one of the cheek sutures may still be fused and the other released.

Although a complete ontogenetic pattern is not available, the proportions of the exoskeletal parts were most likely dependent on the growth stage. The smallest specimen seen, of *P. davidis davidis* from Branch, Nfld. measures about 7 cm along the thorax and pygidium, its outline is narrow and elongated, and carries posterior pleural spines as long as the thorax, much as seen in young individuals of *Olenellus* and *Holmia*.

Teratological malformations are unexpectedly common in the Manuels material. One group of deformities are teratological bumps. Examples of this condition can be seen in the cephalon of a specimen of *P. d. davidis* (Pl. 5, Fig. 6) and on two pleurae of a *P. d. trapezopyge* (Pl. 6, Fig. 8) and several other occurrences were observed. Such bumps may possibly represent a pathological condition. Deformations of the pleurae are more common but have only been found in *P. d. trapezopyge* and *P. d. intermedius*. Among reasonably complete specimens of these two subspecies, almost 1/3 show some kind of pleural deformities, commonly more than one in a single individual. The long most posterior thoracic spines are abruptly terminated in several specimens (e. g. Pl. 6, Figs. 1,5; Pl. 9, Fig. 2). In other cases several adjoining pleurae may be much shortened (Pl. 9, Figs. 1,3). In one of these specimens (Pl. 9, Fig. 3) there are only 18 thoracic tergites, the first two of which are fused together. In one case one of the genal spines is missing and the genal corner bluntly truncated. In particular the case of several adjoining deformed pleurae as in Pl. 9 Fig. 1, 3 may give the impression that the deformities may have been caused by the biting of attacking carnivores, however the unusually high occurrence of this type of teratologies concentrated in mutant subspecies, is suggestive of a genetic origin.

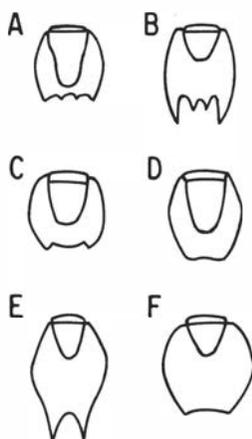


Fig. 8. Phenotypic variation in species of *Eccaparadoxides*, as expressed by pygidial morphology. A – D pygidia of *E. oelandicus* plexus form WESTERGARD (1936). A, *E. oelandicus*, B, *E. quadrimucronatus*, C, *E. bidentatus*, and D, *E. pinus*. 17 thoracic segments are present in *E. oelandicus*, 19 in *E. pinus*, while this number in B and C is unknown. E – F, pygidia of *Eccaparadoxides brachyrhachis* (?) plexus. E, *E. brachyrhachis*, F, *E. mediterraneus*, as reconstructed by LOTZE & SDZUY (1961).

Possible phenotypic variation in other paradoxidids.

Two morphological types of pygidia occur in the Scandinavian *Paradoxides forchhammeri* ANGELIN, according to both BRØGGER (1878) and GRÖNWALL (1902). Remarkably enough, these two types correspond almost exactly to those encountered here respectively in *P. d. trapezopyge* and *P. d. intermedius* at Manuels. LOTZE & SDZUY (1961) reported the co-occurrence in Spain of *Eccaparadoxides brachyrhachis* (LINNARSON) and *E. mediterraneus* (POMPECKJ) which seems to be identical except for the shape of the pygidium, drawn out into paired spines in the former but bluntly terminated in the latter (see Fig. 8 E, F). In Scandinavia, *E. brachyrhachis* occurs without any associated »dual« form. The labral plate (hypostome) figured by LOTZE & SDZUY (1961, Pl. 20, Figs. 10–13) is distinctly different from that figured by BRØGGER (1878, Pl. 2, Fig. 2). Either BRØGGER's determination of the labral plate is wrong, or the Mediterranean form is distinct from *E. brachyrhachis*. Anyhow our evidence concerning *P. davidis* may lead to regard the two species reported to co-occur in Spain as actually representing another example of wide intraspecific variation.

Still another case of probable intraspecific variation is provided by the Scandinavian forms *Eccaparadoxides quadrimucronatus* (WESTERGARD) (with narrow pygidium), *E. oelandicus* (SJÖGREN) (pygidium of intermediate width), and *E. bidentatus* (WESTERGARD) (wide pygidium). These forms have at least one pair of pygidial spines. A fourth form, *E. pinus* (WESTERGARD), has a narrow pygidium without spines. All four forms seem practically indistinguishable except for the pygidium and possibly the last thoracic spines (see Fig. 8 A – D, cf. WESTERGARD 1936). WESTERGARD mentions that the thoracic segments number 17 in *E. oelandicus* and 19 in *E. pinus*, which may seem to set the two forms apart as distinct species. However, our evidence from *P. davidis* shows that such intraspecific variation is entirely possible. It is conceivable that the two extra segments in *E. pinus* may correspond to the two pairs of pygidial spines in *E. oelandicus*. In *E. quadrimucronatus* and *E. bidentatus* the number of segments is unknown. The four forms occur more or less together in Sweden, but the geographic and stratigraphic ranges do not coincide exactly (cf. WESTERGARD 1936, p. 36–37).

Discussion

One of the most remarkable features of the »local« rock column at Manuels and immediate surroundings is that *Paradoxides davidis* occurs at three different stratigraphic levels, separated by intervals in which the other forms regarded here as distinct subspecies are found, (Fig. 1, 4, 9). Even if limited to a local section and to the fate of a particular faunal member, we feel that we are presented precisely by several of the questions and predictions contained in the discussion of the model of punctuated equilibria by ELDREDGE & GOULD (1972) and in particular in their recent reconsideration of the problem (GOULD & ELDREDGE, 1977). Granted that our evidence is lacking characters of generality and the statistics which would be required to provide any significant test of this model, we still find in the issue raised by ELDREDGE & GOULD a most rational framework for the discussion of our observations.

Borrowing at times the terminology of ELDREDGE & GOULD, we note first of all the occurrence, in our section, of several well defined morphological breaks in the fossil record. The new subspecies *Paradoxides davidis trapezopyge* and *Paradoxides davidis brevispinus* appear suddenly in the strata. Their disappearance is also sudden, at least in the case of *P. d. brevispinus*, and particularly revealing in the case of *P. d. trapezopyge*. The new element which appears in the observed sequence of events is the fact that

we are not dealing only with a morphological break, in ascending order, between ancestor and descendant, but in at least two occurrences, between descendant and ancestor.

Are we observing within a local section, simultaneous evidence for the two most important predictions by GOULD & ELDREDGE (1977): sudden transition from ancestor to descendant, as well as relative stasis, documented here by the periodic replacement of the descendants, by the same ancestral stock? We will try to argue that this is most probably the case.

Morphological breaks and geographic speciation. The detailed study of the lithology of the section has shown that to some degree the boundaries between subspecies ranges and particular lithologies coincide (Fig. 1, Table 1). The vertical profile of the different beds and to some extent their mineralogy suggest different local depositional environments. The breaks in the fossil record are indeed real: they are either associated with very rapid environmental changes or, more likely, with interruptions in a particular depositional regime and resumption of the same, at a later time, under different conditions. Although we are dealing with a conformable sequence of strata, the overall body of evidence favors intermittent sedimentation. Indeed, this is a well known situation from e. g. the Cambrian shales of Scandinavia. The local section then is in our case providing a sequence of faunal snapshots, rather than a continuous sampling. In fact even within individual beds, the concentration of undisturbed exuviae within individual laminae, interleaved with often barren strata, conveys the same notion, that the fossil record is made of particular events, rather than of a continuous accumulation of trilobite remains over a long time span. In view of the above, one might argue that the observed morphological breaks are just the result of the imperfect fossil record and that the phenotypic variations in *Paradoxides davidis* may have been the expression of an evolutionary trend in fact more gradual than observed. Since the environment need not have changed so abruptly, (we only observe snapshots separated by unknown time gaps), there might have been enough time for adaptive variations in the local population to explain the sequence of morphological shifts at the subspecies level.

This gradualistic interpretation can be disproven with a fair degree of objectivity in our case. If we were to explain the appearance of *P. d. davidis* at three levels, separated by two beds each represented by different subspecies, it would be preferable if at least some consistency could be found between the images one can construct of the habitat from the lithology and the faunal member observed. We do observe instead *P. d. davidis* in lithologies which seem to imply rather different physical substrates (e. g. the 10–40 cm and 720–750 cm black shale versus the 215–236 cm calcareous shale). Furthermore, we know of two levels with very similar lithologies (the rhythmities of the 155–175 cm and 241–278 cm beds). Yet these two levels are respectively populated by *P. d. brevispinus* and *P. d. trapezopyge* which differ rather drastically in their morphological departures from *P. d. davidis*. More importantly, such departures are non-directional, wider pygidium in one case, shorter pleural spines and coarser ornament in the other, such as to suggest independent, possibly genetic origin. This hypothesis is further supported by the fact that several of those characters developed by the mutant subspecies appear again at a later time, incorporated in *P. fochhammeri*.

We are led then to formulate a different model for the sequence of events observed, one which accounts simultaneously for the detected changes in the depositional environment, coincident with the appearance of mutant subspecies, and the repeated return to the ancestral morphology. This is illustrated in Fig. 9. The model involves the persistence of *P. d. davidis* (relative stasis) outside the southeastern Newfoundland area, most probably in the west

European region, throughout the entire time sequence encompassing the observed events. Manuels is representative of an area which became intermittently isolated from the main *P. d. davidis* geographic range. During such periods of isolation indigenous subspecies evolved from the type subspecies, first *P. d. trapezopyge*, then *P. d. brevispinus*. This interpretation then favors regarding the area represented by Manuels as a peripheral isolate where rapid speciation could have set in. When contact was re-established, the type subspecies may have reinvaded the area. In one case, the return of *P. d. davidis* after the establishment of *P. d. trapezopyge*, we even have clear evidence of a contact zone of secondary intergradation, the hybrid form being represented by *P. d. intermedius*. In this connection it is relevant to note that the trend of *P. d. trapezopyge* to exhibit teratologies is carried over to *P. d. intermedius*, which shows the same kind of malformations with a comparatively high rate of occurrence.

In Fig. 9, the section depths where breaks in the sedimentary and morphological sequence have been observed, are labelled as »possible sites of bathymetric shift«. In two of such occurrences invasion by *P. d. davidis* is suspected. Although it cannot be conclusively proven, it is quite possible that both the interruptions and changes in the sedimentary regime and the suggested faunal migrations may have been caused by bathymetric shifts. As already mentioned previously, there is indeed independent evidence (see section on lithology) which indicates that a widespread regression of perhaps tectonic origin was responsible for the extinction of *P. d. davidis* after its last reappearance in the sequence.

Our evidence then supports a model of allopatric geographic speciation, in spite of the notion that morphological breaks are associated with an imperfect, discontinuous fossil record. **Stasis:** As repeatedly emphasized by ELDREDGE & GOULD (1972, 1977), »Stasis is data«. We are in a position to give a somewhat limited, but still relevant set of such data in relation to the comparative persistence of the morphological characters of *P. d. davidis* throughout its stratigraphic and geographic range. We have been led to postulate that allochronic recurrences of *P. d. davidis* in the local rock column at Manuels have been the result of migrations from some geographic area to be regarded as the depository of the main gene pool of the type species. We know that the geographic range of *P. d. davidis* extended to Britain, Scandinavia, possibly to Spain and clearly also to the Avalon peninsula and Nova Scotia.

Relevant here is the fact that an intraspecific differentiation of subspecies similar to what is found at Manuels is unknown from the European collections of *P. davidis*. The limited collection of material from Wales which we have examined is entirely consistent with its attribution to *P. d. davidis*. A similar conclusion can be drawn from other unmeasured samples from Wales and Scandinavia. A sizeable amount of *P. davidis* material collected recently some 200 km west of Manuels on the Burin Peninsula, southeastern Newfoundland, by Mr. Sean J. O'Brien of St. John's, Newfoundland, also conforms nicely with *P. davidis davidis*, although the specimens are too distorted for meaningful measurement. Only at Kellygrews, about 6 km SW of Manuels, the presence of *P. d. davidis*, *P. d. trapezopyge* and *P. d. brevispinus* could be ascertained, in a vertical succession corresponding to that found at Manuels. We thus have some sampling of the geographic distribution of *P. d. davidis*, whose habitat seems to have been widespread, and some evidence that the speciation phenomena observed at Manuels and Kellygrews were part of a local event. Although we do not have a sequential sampling of *P. d. davidis* from outside the Avalon peninsula, the overall pattern is one of considerable stability in the basic morphological characters of the nominate subspecies, since it is unlikely that all samples examined were contemporaneous. The reappearance of *P. d. davidis* at various levels at Manuels however does represent a

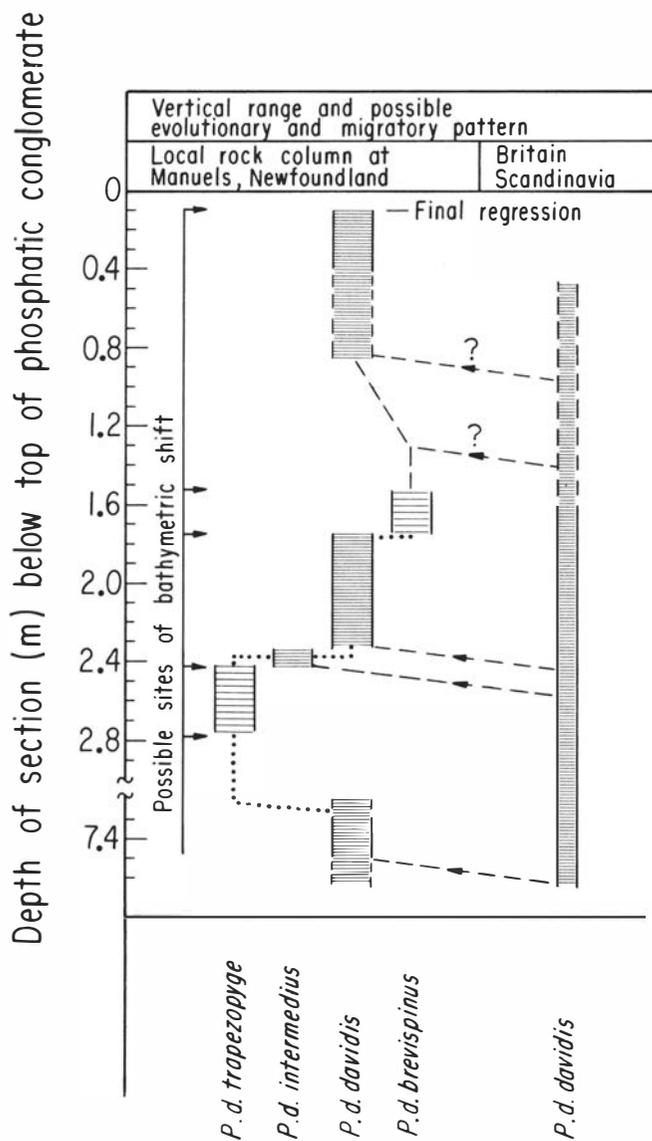


Fig. 9. Interpretation of the pattern of occurrence of different subspecies of *Paradoxides davidis* at Manuels. The Middle Cambrian planetary scenario places southeastern Newfoundland not far off the coast of Spain, along an arc encompassing Maritime North America, Britain and Scandinavia. It is postulated that the main gene pool of *P. davidis* may have been located at some distance from southeastern Newfoundland, but still intermittently in contact with the latter through e. g. larval migration. The continuity of this gene pool, represented by *P. d. davidis*, is indicated by the vertical column at the right of the figure. When the connection with the main gene pool was interrupted, mutation and natural selection in the Newfoundland isolate led to the complete dominance of the subspecies *P. d. trapezopyge*. We have no record of this transition. We have a record however of the reappearance of *P. d. davidis*, most likely through a new migration, possibly induced by a bathymetric shift. After a short time of interbreeding (or e. g. the sweeping of a hybrid belt through the site), the local subspecies was completely substituted by the ancestral subspecies. Interbreeding or hybridization (secondary intergradation) is suggested by the appearance of *P. d. intermedius* in a thin horizon between the two ranges. Later on, a new period of isolation may have occurred, enabling the establishment of a new local subspecies, *P. d. brevispinus*. Later and for a third time in the sequence, *P. d. davidis* returned to arrest the incipient process of speciation, and to survive to the end of the *P. davidis* range at Manuels. Several of the characters developed by the subspecies of *P. davidis* will reappear however at a later time, incorporated in a subsequent species, *P. forchhammeri*.

sampling of the stability of this subspecies with time and we can set limits as to the extent of gradual variations which may have occurred. In fact, with the suggestion that reappearance may be due to immigrations from the main geographic range, we may be generally sampling the stability of the *P. d. davidis* stock at a more general level than the local rock column.

The mean values and standard errors of the mean of the ratio of pygidial width W_2/W_1 for various samples of *P. d. davidis* are given in Table 2 (see also Fig. 4b). The table contains such values also for the other subspecies of *P. davidis* and for *P. forchhammeri*.

It does seem that over essentially the entire vertical range of *P. d. davidis* (9.4 m, of which the top 7.5 m have been sampled) there may have been at most a gradual increase in W_2/W_1 , from about 0.73 at the lowest level to 0.99 near the end of the range, while all other morphological characters remained essentially constant.

Subspecies	Sample a) origin	Mean value	Standard error of mean	Number of specimens
<i>P. d. davidis</i>	Wales	0.81	0.03	8
<i>P. d. davidis</i>	10–40 cm	0.99	0.04	10
	175–215 cm	0.87	0.03	30
	215–236 cm	0.91	0.04	7
	720–750 cm	0.73	(0.1)	2
<i>P. d. brevispinus</i>	155–175 cm	0.75	0.02	19
<i>P. d. intermedius</i>	236–241 cm	1.16	0.03	16
<i>P. d. trapezopyge</i>	241–278 cm	1.50	0.015	58
<i>P. forchhammeri</i>	Sweden	1.56	(0.12)	3

a) Ranges in cm represent depth intervals in the Manuels section.

Table 2. Mean values of the ratio of pygidial widths W_2/W_1 for various samples of *P. davidis* and for *P. forchhammeri*.

Such slow trend toward expansion of the posterior end of the pygidium culminates at the 10–40 cm level, as can be appreciated visually from the plates (see e. g. Pl. 5, Fig. 4, 9, 10). The sample from Wales yields a ratio of 0.81, comfortably inside the range of variation observed at Manuels.

We thus have some measure of the extent of stasis in the biometric parameter more subject to phenotypic variation, throughout the life span of *P. davidis davidis*. A directional variation as gradual and limited as observed could possibly be accounted for in terms of non-genetic morphological drift, possibly adaptive in origin.

We reach the conclusion that the model of punctuated equilibria of ELDREDGE & GOULD (1972, 1977) does provide a reasonable account of the present sequence of occurrences. Quoting from these authors: »The norm for a species during the heyday of its existence as a large population is morphological stasis, minor non-directional fluctuation in form, or minor directional change bearing no relationship to pathways of alteration in subsequent daughter species. In the local stratigraphic section we expect no slow and steady transition, but a break with essentially sudden replacement of ancestor by descendants: this break may record the extinction or migration of a parental species and the immigration of a successful descendant rapidly evolved elsewhere in a small, peripherally isolated population«.

These two predictions have relevant implications when related to our example, provided the full range of possible events which the model encompasses is taken into account. In particular, these must include the possibility that not all allopatric descendant species may be successful and that the latter may be repeatedly replaced by the ancestral species, as the record of events in the Manuels rock column seems to suggest.

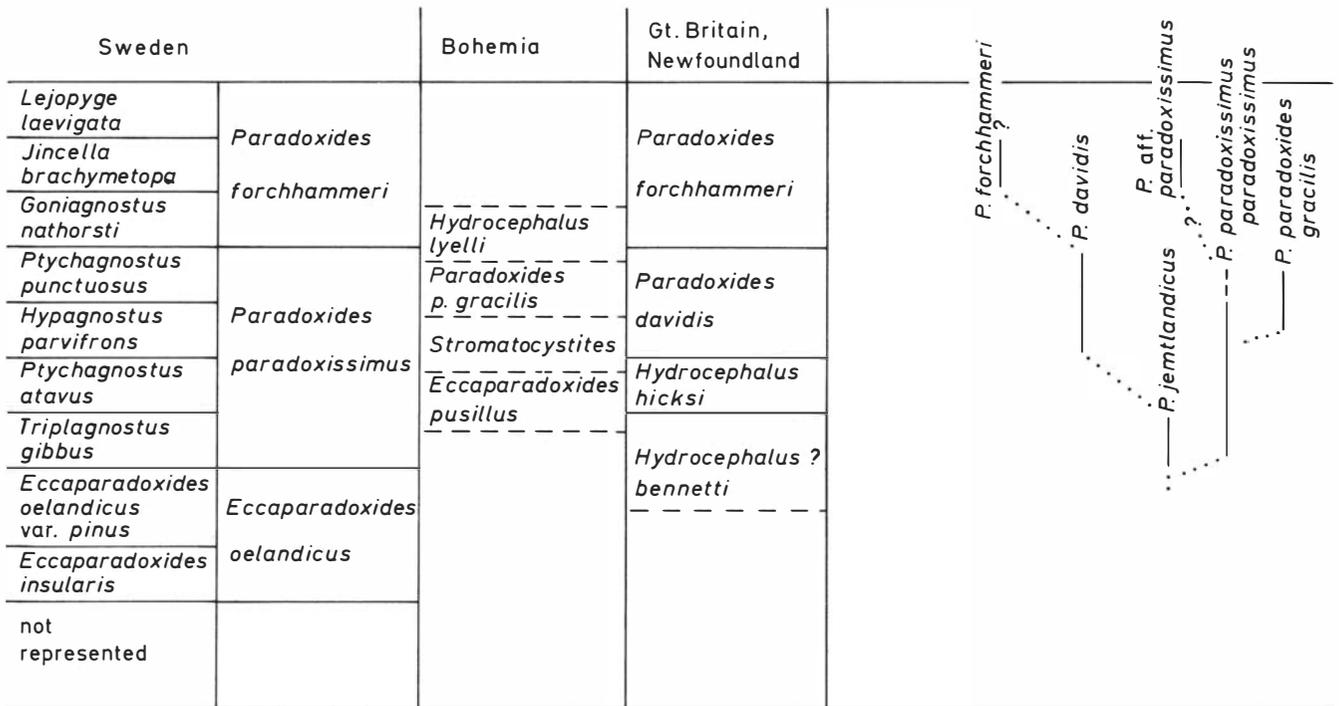


Fig. 10. Diagram showing Middle Cambrian correlations (partly after JELL 1974) and the suggested phylogeny of species of *Paradoxides* s. s. The Bohemian subspecies should read *P. paradoxissimus gracilis*.

Evolution within the genus *Paradoxides*

As defined in the Treatise on Invertebrate Paleontology (POULSEN 1959), the genus *Paradoxides* is fairly wide and heterogeneous. In the type species, *P. paradoxissimus*, and most others as far as known, the labral plate is fused with the rostral plate to form a rostro-labral plate. In contrast with the condition in at least most species of *Hydrocephalus* and *Eccaparadoxides* (= *Acadoparadoxides* and *Phanoptes*, nom. obl.), the last thoracic pleural spines extend typically far behind the pygidium. The stratigraphic sequence of occurrences of the best known *Paradoxides* species can be extracted from the Middle Cambrian correlations shown in Fig. 10 (partly after JELL 1974). The ranges and a suggested phylogeny of species are also indicated in this figure, and the phylogenetic diagram of Fig. 11 gives a pictorial representation of our conjecture.

The earliest known members appear to be *P. jemtlandicus* WIMAN and *P. paradoxissimus* WAHLENBERG. Of these, the former seems to be the most primitive in general appearance. An example is shown in Pl. 9, Fig. 4. The glabella exhibits transverse furrows S1 and S2, the latter faint. The thorax has 19 segments, and the pleural spines are comparatively short, although the last pair distinctly extend beyond the posterior edge of the pygidium. The pygidium is rounded in outline, with rhachis marked by one distinct axial ring and faint traces of one or two additional ones. The posterior border does not appear to be arched. It is not known if the labral and rostral plates were fused. *Paradoxides paradoxissimus paradoxissimus* is equally old, but may be somewhat more advanced. S1 and S2 are both transverse and equally impressed. The thorax, with 21 segments in a few complete specimens, carries long pleural spines, the second pair being slightly prolonged, a reminiscence from the long macrospines of the larvae. The pygidium has a distinctly segmented rhachis surrounded by a flat border. It is easy to imagine how this species could have evolved from *P. jemtlandicus* or a similar species through a few small morphological steps. Late in *P. paradoxissimus* times, *P. gracilis* (BOECK) occurred in Bohemia. This form is virtually indistinguishable from *P. paradoxissimus* except in the thorax which as far

as known has only 20 segments. Considering the evidence on variation within other paradoxidids, this difference is however not even necessarily of subspecific value, but as the two forms are geographically separated, the Bohemian form may in this case be distinguished as *P. paradoxissimus gracilis*. Aside possibly from *P. aff. P. paradoxissimus* reported by WESTERGÅRD (1953, p. 36) from *P. forchhammeri* beds, this line does not seem to lead any further. *Paradoxides davidis* SALTER is known only from late *P. paradoxissimus* times. The typical form has a glabella with well developed S1 and S2, the course of the latter being characteristically sinuous, and only occasional traces of additional anterior furrows may be present. The thorax, as seen above, has predominantly 20 segments, of which the last is commonly fused with the pygidium. The pleural spines are long, the posterior ones in particular, so that the thorax is more or less parallel-sided. The segmentation of the pygidial rhachis is similar to that of *P. jemtlandicus*, and a diagnostic character is found in the arching of the slightly concave posterior border. The outline of the pygidium is different from that in *P. paradoxissimus*, but a derivation from *P. jemtlandicus* is still quite conceivable. The steps involved consist only of a widening of the border and truncation and arching of the posterior margin. In addition, the pleural spines, in particular the last pair, need be prolonged and S2 be made stronger. Indeed, in view of the variability established here for *P. davidis*, morphological shifts such as these seem quite acceptable. It is quite conceivable that multiplication of species leading respectively to *P. paradoxissimus* and *P. davidis* may have occurred in peripheral isolates of *P. jemtlandicus*, beginning with material extracted from the same gene pool.

As repeatedly noted in the previous sections, the overall morphology of *Paradoxides forchhammeri* ANGELIN is very reminiscent of that of *P. davidis trapezopyge*, but for the ornamentation which is closer so that of *P. d. brevispinus*. Although no complete specimen of *P. forchhammeri* is available, we have attempted a new reconstruction of this trilobite, based in part on fragmentary material, in part on previous drawings, notably from BRØGGER (1878), and on our knowledge of the basic structure of true paradoxidids. Unknown is the number of thoracic tergites,

as the reconstruction by ANGELIN (1878) could not be traced to any existing complete specimens. It is a reasonable guess that the number may be close to 19–20. Our reconstruction is shown in Fig. 7d, where it can be compared with the subspecies of *P. davidis*. With a few exceptions the similarities of the two species are overwhelming and our study of the subspecies of *P. davidis* shows how characters such as the wide pygidium and the coarse ornamentation developed already in this species which we believe was ancestral to *P. forchhammeri*. One distinct difference however exists, consisting in the presence, in *P. forchhammeri*, of pronounced interrupted S3 and S4 glabellar furrows, anterior to S2. Only faint traces of such furrows have been seen in *P. davidis*. This seems to conflict with the commonly accepted idea that the glabellar furrows had the tendency to become obliterated in some trilobites and never reoccurred from a virtually smooth surface. Quite to the contrary instead, we observe in the true paradoxidids a progressive deepening and multiplication of the glabellar furrows. In this connection we suggest that since the furrows are only one facet of the segmentation and muscular arrangement, as long as these features and the underlying genetic information are not lost it seems quite possible for the furrows or parts of them to reoccur. After all, much of the genetic basis for their formation may be preserved even if they are not expressed, perhaps due to the suppression of the responsible structural gene(s) (VALENTINE & CAMPBELL 1975).

Paradoxides paradoxus (LINNÉ), represented by only one specimen, may be a distinct species of *Paradoxides*. The original drawing by LINNÉ (1753, Mus. Tess. Tab. III, Fig. 1) is too primitive to be of any help in identification. Although assimilated by BRONGNIART (1822) with *P. paradoxissimus*, its appearance from ANGELIN's subsequent description (ANGELIN 1878, App., Tab. I) is quite incompatible with such an identification. Although the specimen could not be traced as yet, a photograph of it is available (NATHORST 1907). Notwithstanding the rather poor state of preservation of the specimen, 20 tergites can be counted. The glabella is crushed showing the underlying labral plate, seemingly indistinguishable from that of *P. davidis*. The cranidium and free cheeks seem displaced toward the thorax, overlapping the first two tergites. The pygidium is expanded posteriorly, much as in *P. davidis trapezopyge* and *P. forchhammeri*. Lacking however the critical information provided by the glabellar furrows, it seems impossible to distinguish between these two possible alternatives, among others. Unless examination of the specimen may become feasible, further speculation as to possible phylogenetic position of this trilobite would be too doubtful.

Also doubtful is the position of *Vinicella desiderata* (BARRANDE), known only from its pygidium with segmentation reminiscent of *P. paradoxissimus* and perhaps a posterior arch as in *P. davidis*. Disturbing is the presence of marginal spines, directed obliquely backwards, on the lateral borders of the pygidium, one of the reasons which induced SNAJDR (1958) to propose the new generic assignment of this trilobite.

Summary and conclusions.

The morphology of *Paradoxides davidis* at Manuels, SE Newfoundland, is much more varied than at any other occurrence as far as known. A bed-by-bed study of the exuviae of this trilobite in the local rock column reveals two major classes of morphological variation. The first class involves events of non-directional, intraspecific phenotypic shifts, occurring in a vertical succession (allochronic variation). Such characters as the shape of the pygidium and last pair of pleural spines, or the length of the thoracic pleural spines and ornament are affected in these events. The second class involves random variability of certain morphological characters within any one stratigraphic level (and presumably population).

The events of phenotypic variation occur in a remarkable sequence. Lowest in the section is the typical form *P. davidis davidis*, as known from the type locality in Wales. After an interval without recorded determinable specimens a wide-tailed form occurs, distinguished here as a new subspecies, *P. davidis trapezopyge*. Above a thin horizon with an intermediate form, *P. d. intermedius*, typical *P. d. davidis* recurs, only to be followed by a bed populated by another new subspecies, *P. d. brevispinus*. This form has a pygidium which tends to be even narrower than in *P. d. davidis* and, more characteristically, a granulation almost as coarse as in *P. forchhammeri* and comparatively very short pleural spines. After the disappearance of this subspecies, *P. d. davidis* reoccurs for a third time and extends to the top conglomerate, which may indicate a period of regression of the sea. Except for *P. d. brevispinus*, the diagnostic criterion adopted in distinguishing the different subspecies is the ratio between posterior and anterior widths of the pygidium.

The random morphological variability concerns more prominently the number of thoracic segments, seen to vary from 18 to 21, and the presence or absence of fusion between the pygidium and the last thoracic segments. There is also a strong component of teratologies, such as abortion of pleural or genal spines and occasional fusion of thoracic tergites, observed to affect *P. d. trapezopyge* and *P. d. intermedius*.

The enclosing sediments are fine grained silty shales. A study of the vertical profile and mineralogy of the sediments has revealed likely variations in the depositional environment correlated with the phenotypic replacements referred to above. A general pattern of intermittent sedimentation has emerged in which depositional discontinuities coincide with boundaries between subspecies ranges.

Notwithstanding the existence of morphological breaks associated with possible interruptions of sedimentation, morphological replacements such as those by *P. d. trapezopyge* and *P. d. brevispinus* cannot with any degree of plausibility be attributed to gradual adaptive radiation due to habitat changes, in view both of the non-directional nature of the phenotypic variation and of ensuing inconsistencies with the lithological evidence.

Instead, the pattern of phenotypic change in the local rock column at Manuels finds a natural interpretation in terms of events of rapid allopatric geographic speciation, as well as of comparative morphological stasis of the parental species, much as envisaged in the predictions of the model of punctuated equilibria by ELDREDGE & GOULD (1972, 1977). Thus the recurrence of *P. d. davidis* may be explained as the result of intermittent contact with and immigration from other areas populated by an essentially static gene pool. Such areas were likely represented by Wales and Scandinavia, where only the typical subspecies of *P. davidis* has been identified. In comparison with such areas, the local habitat of Manuels and surrounding area should be characterized intermittently as a peripheral isolate, where rapid and nondirectional events of speciation could take place. We attribute *P. d. trapezopyge* and *P. d. brevispinus* to two independent such events of allopatric geographic speciation, both of which were apparently aborted (at least locally) by the reestablished contact with the main ancestral gene pool. Such contact could have resulted in a zone of secondary intergradation, of short duration if the contact was effective. In one of such occurrences, the transition from the mutant *P. d. trapezopyge* to the recurrent ancestor *P. d. davidis*, we do in fact detect a narrow horizon (5cm) separating the ranges of these two subspecies, which is populated by the seemingly hybrid *P. d. intermedius*. Morphological stasis in *P. d. davidis* could also be tested throughout most of its stratigraphic range with the conclusion that only a minor gradual shift in pygidial morphology may have indeed occurred throughout the life span of this widespread phenotypic unit.

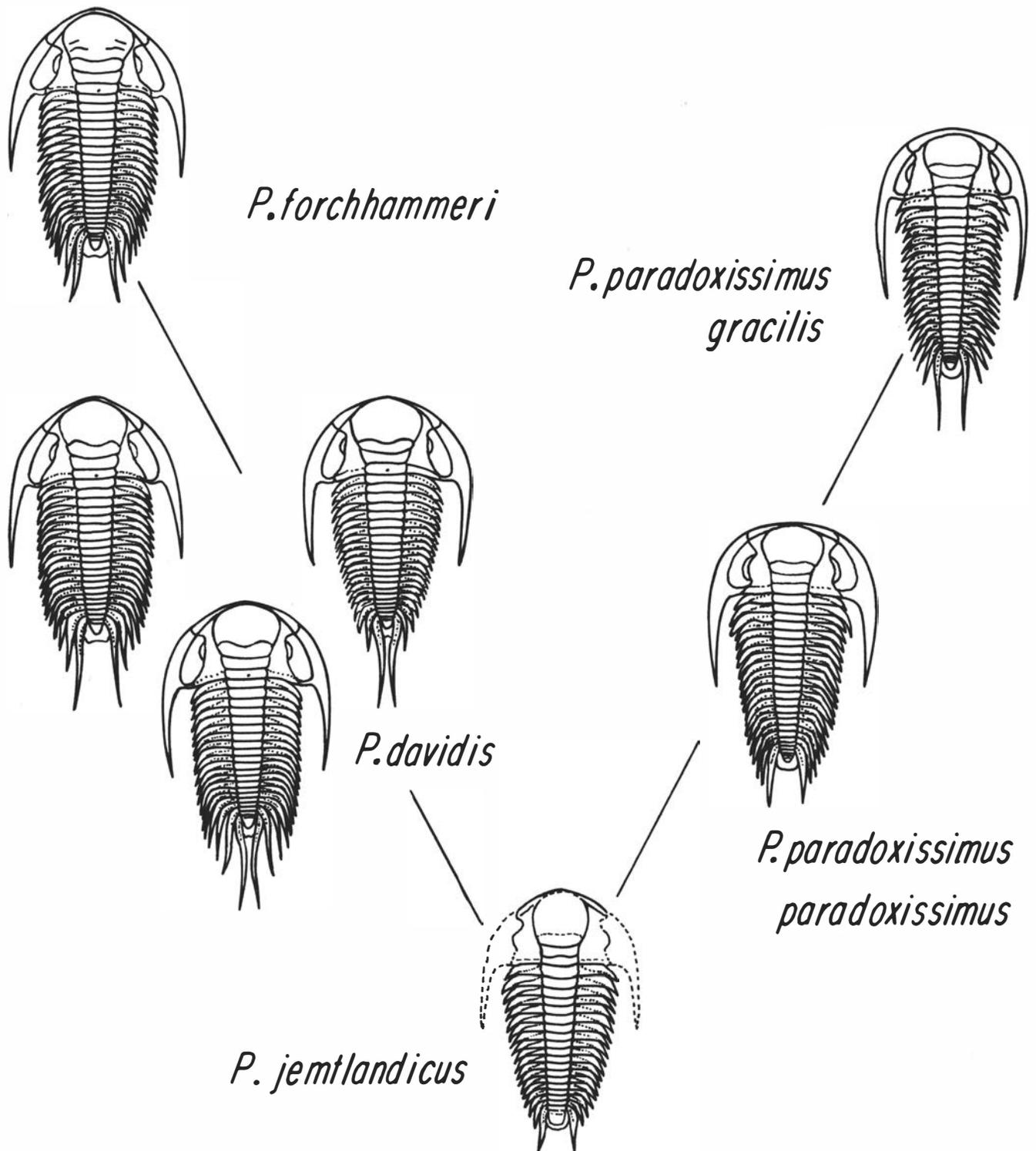
Possible phylogeny of *Paradoxides* s.s.

Fig. 11. Pictorial diagram illustrating the evolution of the genus *Paradoxides*. See also Fig. 9. The only noticeable evolutionary trend between the different species seems to involve a strengthening of the second glabellar furrow S2 and the progressive appearance of distinct additional glabellar furrows S3 and S4. The genus *Paradoxides* may have evolved from *Hydrocephalus* through the fusion of the labral and rostral plates.

We note that the shape of the pygidium of *P. d. trapezopyge* and the comparatively coarser granulation of *P. d. brevispinus* are features characteristic of the younger species *P. forchhammeri*.

These characters in particular and other strong similarities suggest a close phylogenetic relationship between *P. forchhammeri* and *P. davidis*. It is not known whether any of the two new subspecies of *P. davidis* were directly involved in the speciation of *P. forchhammeri* or if the same characters developed independently in another lineage leading from the former to the latter species.

Nevertheless it is tempting to qualify the two events of phenotypic variation observed in *P. davidis* as »incipient speciation«.

Oddly, the younger *P. forchhammeri* exhibits deep glabellar furrows S3 and S4, usually absent or occasionally weakly developed in the older *P. davidis*. This is perhaps the first known case of trilobites showing, in the phyletic lineage, the reappearance of almost lost glabellar furrows.

Partly based on the new evidence provided by *P. davidis*, the evolution of paradoxidids with a fused rostro-labral plate, i. e. *Paradoxides* s. str., is discussed. *P. jemtlandicus* may represent a primary stock from which *P. davidis* and *P. paradoxissimus* may have radiated as two separate lineages. *P. gracilis* differs from *P. paradoxissimus* only in the number of thoracic segments (so far as these are known), and we prefer to regard it as a subspecies of the latter. *Vinicella desiderata*, known only from its pygidium, shows similarities to *P. davidis* and *P. paradoxissimus* and may belong to the same group of paradoxidids.

The phenotypic diversity of some other paradoxidids is also discussed. Particularly well known to us is the *Eccaparadoxides oelandicus* plexus, which in addition to the type form also includes *E. quadrimucronatus*, *E. bidentatus* and *E. pinus*. These forms differ in pygidial shapes and number of thoracic segments (known only in two of the forms). From the behavior of these morphological characters in *P. davidis* and from the circumstance that there is an intergradation between the known forms (the material in the museum of the Geological Survey of Sweden shows even more intergradation than evident from the illustrations of WESTERGÅRD 1936), we consider the entire plexus as belonging to a single species.

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Action to protect the *Paradoxides* beds at Manuels under the Section 2 of Historic Objects, Sites and Records Act, Chapter 153, R. S. N. 1970, has recently been taken by the Newfoundland Ministry of Provincial Affairs, in conjunction with the Canadian Department of Mines and Energy.

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Abbreviations in plate explanations.

BM British Museum (Natural History), London.
FMNH Field Museum of Natural History, Chicago
Gr I Grant Institute of Geology, Edinburgh.
LM Department of Geology, University of Lund.

Plate 1

Vertical profile of the sediments near the top of the *Paradoxides davidis* range, on the east side of the Manuels River. Polished sections photographed while immersed in xylene, on the left hand side at 2/1, on the right hand side at 5/1. Depths in section are measured from the top of the conglomerate layer marking the end of the *P. davidis* range.

Fig. 1, 2: Fine parallel laminations in the black shale from the 10–40 cm depth interval. Dominant *Paradoxides* member at this level is *Paradoxides davidis davidis*. FMNH B554 (Biostratonomy Collection).

Fig. 3, 4: Grey-greenish to black graded rhythmites characteristic of the 155–175 cm depth interval. This bed contains almost exclusively *P. davidis brevispinus*. The profile of sectioned trilobite exoskeletons causes apparent waviness and irregularities. FMNH B555.

Fig. 5, 6: Lenticular bedding, coquina of trilobite exoskeletons, bioturbated laminae in the slightly calcareous shale at the 215–236 cm level. Dendritic pattern most likely of diagenetic origin. This layer is populated by *P. davidis davidis*. FMNH B556.

Fig. 7, 8: Section through the 236–241 cm layer, characterized by a population of *P. davidis intermedius*. This layer marks the transition from the overlying *P. davidis davidis* bed to the underlying *P. davidis trapezopyge* bed. FMNH B557.

Fig. 9, 10: Grey-greenish to black graded rhythmites of the 241–278 cm bed, populated by *P. davidis trapezopyge*. Large complete trilobite exuviae occur in the lighter laminae embedded in the darker band at the center of Fig. 9. FMNH B558.

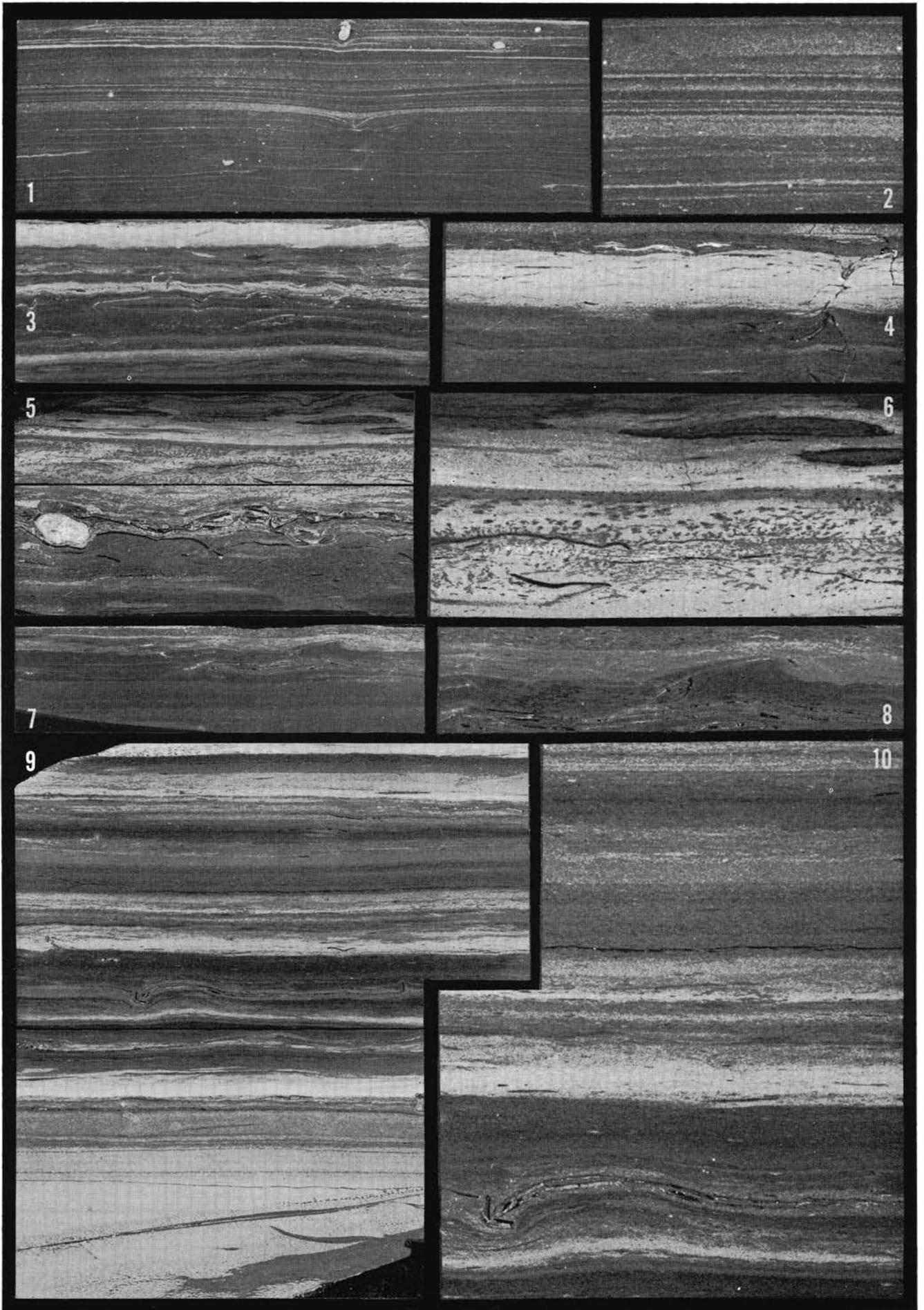


Plate 2

Paradoxides davidis davidis from the type locality Porth-y-rhaw, St. Davids, Pembrokeshire. All 0.57/1, except Fig. 4.

Fig. 1: Almost complete exuviae with 20 thoracic segments. Photographed from cast. BMI 1.

Fig. 2: Pygidium and posterior part of thorax with strong relief, partly compressed laterally. Gr. I 44951.

Fig. 3: Free cheek, photographed from latex replica. Gr I 44943

Fig. 4: Section, photographed in xylene, of the sediments containing the specimen in Fig. 2. FMNH B 559. 2/1.

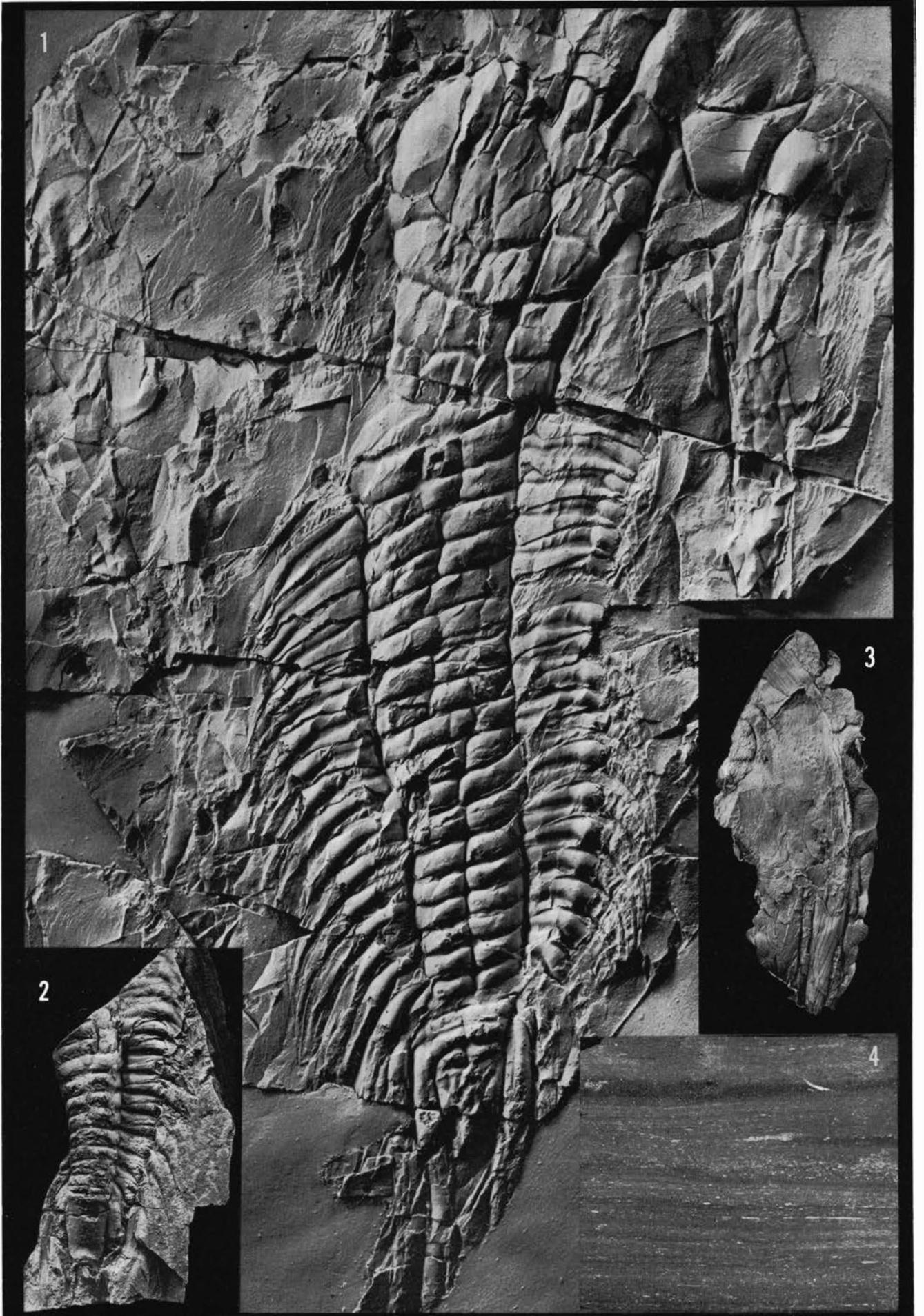


Plate 3

Paradoxides davidis davidis from the type locality Porth-y-rhaw, St. Davids, Pembrokeshire. All 1/1.

Fig. 1: Substantially complete exuviae with 20 thoracic segments, distorted by tectonic shear. Rhachis much flattened. Photographed from latex mould with SE illumination. Gr I 44922.

Fig. 2: Exuviae showing most of one half of the thorax with pleural spines, one free cheek with genal angle, part of the glabella and of the labral plate. The ornamentation includes terrace lines on the cephalic doublure and labral plate, tubercles, and vascular ridges on the pleurae. Exterior impression, photographed from latex replica. Gr I 44921.

Fig. 3: Portion of the long posterior pleural spines. Latex replica. Gr I 44946.

Fig. 4: Rostro-labral plate with terrace lines. Latex replica. Gr I 44938.

Fig. 5: Pygidium and posterior portion of thorax with long spines. Note how spines converge behind pygidium. Latex replica. Gr I 44924. 1.5/1.



Plate 4

Paradoxides davidis davidis from Manuels River, Newfoundland. All except Fig. 1, 1/1.

Fig. 1: Posterior region of largest exuviae found. The first segment of the pygidium is well developed, and its pleural portion is clearly visible on the right side, where even a pleural furrow can be seen. The pleural portion of the segment is posteriorly extended into a spine-like lobe, making this pygidium more deeply indented than any other in the collection. Section 215–236 cm. FMNH PE 25538. 0.6/1.

Fig. 2: Incomplete thorax. External impression under SE illumination (photographic replica). Section depth 10–40 cm. FMNH PE 28963 B.

Fig. 3: Pygidium and fused last thoracic tergite. Pygidium has unusually distinct segmentation. Section depth 215–236 cm. FMNH PE 25540 A.

Fig. 4: Posterior region of thorax with pygidium. Section depth 10–40 cm. FMNH PE 28964 A.

Fig. 5: Parallel sided pygidium fused to last thoracic tergite. Section depth 10–40 cm. FMNH PE 28965.

Fig. 6: Rear portion of thorax and distally tapered pygidium. Pleural spines poorly delineated due to surface incrustation by mineral deposit. Section depth 10–40 cm. FMNH PE 28966.

Fig. 7: Posterior half of thorax with parallel sided pygidium. Section depth 10–40 cm. FMNH PE 28967.

Fig. 8: Posterior half of thorax with pygidium slightly expanded distally. This character is observed in several specimens from the 10–40 cm bed (see e. g. Fig. 4, 10). Note distinct long pleural spines and boring on rhachis. Section depth 10–40 cm. FMNH PE 28968 A.

Fig. 9: External impression (photographic replica) of pygidium in Fig. 8, showing better outline of pygidial morphology. FMNH PE 28968 B.

Fig. 10: Pygidium, fused only axially to last thoracic tergite. The only preserved pleural spine is converging toward axis. Lateral borders of pygidium gently convex and expand distally. The ratio W_2/W_1 for this pygidium is 1.23, at the upper end of the distribution for *P. davidis davidis* in the 10–40 cm bed. FMNH PE 25547.

Fig. 11: Small specimen lacking both free cheeks and pygidium with last thoracic tergite. Section depth 175–215 cm. FMNH PE 25539 A.



Plate 5

Paradoxides davidis davidis from Manuels River, Newfoundland. All except Fig. 11, 1/1

Fig. 1: Rear part of body with long spines. External impression (photographic replica). Section depth 175–215 cm. FMNH PE 25127 B

Fig. 2: Posterior thoracic region and tapering pygidium. Last pair of pleural spines converge almost completely. Photographic replica from external impression. Section depth 720–750 cm on the west bank of the Manuels River. FMNH PR 28969 B

Fig. 3: Cranidium, fractured axially by compression. Possibly due to preservation in soft black shale, the furrows and surface ornamentation are particularly distinct in this and other specimens from the 720–750 cm bed on the west bank of the Manuels River. FMNH PE 28970

Fig. 4: Almost parallel-sided pygidium. In this as well as in the specimen of Fig. 5, the last thoracic rhachial ring is fused with the pygidium but the pleurae have been broken away, indicating that they were not fused to the lateral sides of the pygidium. Section depth 175–215 cm. FMNH PE 25541.

Fig. 5: Tapering pygidium. Section depth 215–236 cm. FMNH PE 25542.

Fig. 6: Cranidium. Bump on right side of frontal glabellar lobe probably pathological. Section depth 175–215 cm. FMNH PE 25543

Fig. 7: Rostro-labral plate showing distinct pattern of terrace lines. Photographic replica from external impression. Section depth 215–236 cm. FMNH PE 25120.

Fig. 8: Cranidium, fractured axially by compression. The deformation from this cause and individual variability probably account for the minor morphological differences, in particular in the course of the glabellar furrows, between this specimen and that of Fig. 6. Note suggestion of additional glabellar furrow S3 on right side. Note also ornament: terrace lines on cephalic border and frontal glabellar lobe, small tubercles on fixed cheek, occipital ring, and on glabella, posteriorly to terrace lines. External impression (photographic replica). Section depth 215–236 cm. FMNH PE 25122.

Fig. 9: Posterior region of body. Photographic replica from external impression. Section depth 175–215 cm. FMNH PE 25545.

Fig. 10: Rear part of body. Pygidium parallel-sided. Line about 1 mm from posterior edge of pygidium marks the position of the inner edge of the doublure. Section depth 175–215 cm. FMNH PE 25544.

Fig. 11: Portion of thorax to show ornamentation, consisting of small tubercles concentrated primarily on the most convex surfaces. Photographic replica from external impression. Section depth 175–215 cm. PE 25546 B. 2.5/1.



Plate 6

Fig. 1–7: *Paradoxides davidis intermedius* from Manuels River, Newfoundland. All specimens originate from section depth 236–241 cm.

Fig. 1: Portion of thorax and pygidial region of specimen with 19 thoracic tergites. The right pleura of the last thoracic tergite is atrophic and abnormally terminated. FMNH PE 25551. 1/1.

Fig. 2: Pygidium, fused axially to last thoracic tergite whose pleurae are missing. In this and e. g. Fig. 4 and 5, the pygidial outline is characteristically bell-shaped, with truncated distal corners, intermediate between that of *P. davidis davidis* and *P. davidis trapezopyge*. FMNH PE 28952. 1.5/1.

Fig. 3: Holotype. The thorax is complete with 20 tergites. Pleurae and pleural spines much as in *P. davidis davidis* and *P. davidis trapezopyge* with the exception of the last pair. These, although converging backwards as in *P. d. davidis*, are constricted at the level of the termination of the pygidium, as in *P. d. trapezopyge*. The pygidium is approximately bell-shaped as in Fig. 2. The external impression of the rostro-labral plate is correctly located although the cranium is missing entirely. Note two additional pygidia, both fused to last thoracic tergite, at left center of plate. FMNH PE 28971 A.

Fig. 4: Pygidium, fused axially to last thoracic tergite whose pleurae are missing. FMNH PE 25549. 1/1.

Fig. 5: Pygidium, fused to last thoracic tergite. Both pleurae of the latter are improperly terminated suggesting congenital deformities. The short stub on the right is fused to the lateral margin of the pygidium. The left pleura is underdeveloped and terminates abruptly. Photographic replica from external impression. FMNH PE 25550. 1.5/1.

Fig. 6: Pygidium fused axially to last thoracic tergite, carrying only left pleura and spine. Segmentation of pygidial rhachis unusually distinct. FMNH PE 25548. 1/1.

Fig. 7: Pygidial region with complete last pair of pleural spines. FMNH PE 28972 A.

Fig. 8: *Paradoxides davidis trapezopyge* from Manuels River, Newfoundland. Exuviae with open sutures but with cranium and genal spines roughly in position. Note probable vascular prosopon in fixed and free cheeks and in pleurae. Each pleura has an anterior and a posterior vascular ridge, and a similar ridge is found along the posterior margin of the fixed cheek. Nodular protrusions on right pleura of thoracic tergites 8 and 9 are probably pathological. Section depth 241–278 cm. FMNH PE 25014 A. 0.6/1.



Plate 7

Paradoxides davidis trapezopyge from Manuels River, Newfoundland.
All specimens from section depth 241–278 cm, 1/1.

Fig. 1: Free cheek. The genal angle is slightly damaged. Photographic replica from external impression. FMNH PE 25552 B.

Fig. 2: Holotype. Exuviae with slightly displaced cranidium and free cheeks. One cheek is turned over. Posterior narrow band on pygidium indicates shape of pygidial doublure. FMNH PE 25013.

Fig. 3: Pygidium with last thoracic tergite. Photographic replica from external impression. FMNH PE 25553 B

Fig. 4: Pygidial region of almost complete exuviae. FMNH PE 28973 A.

Fig. 5: Pygidium with posterior narrow band indicating extent of doublure. Small posterior lobes may represent the distal tip of pleural segments. FMNH PE 25554.

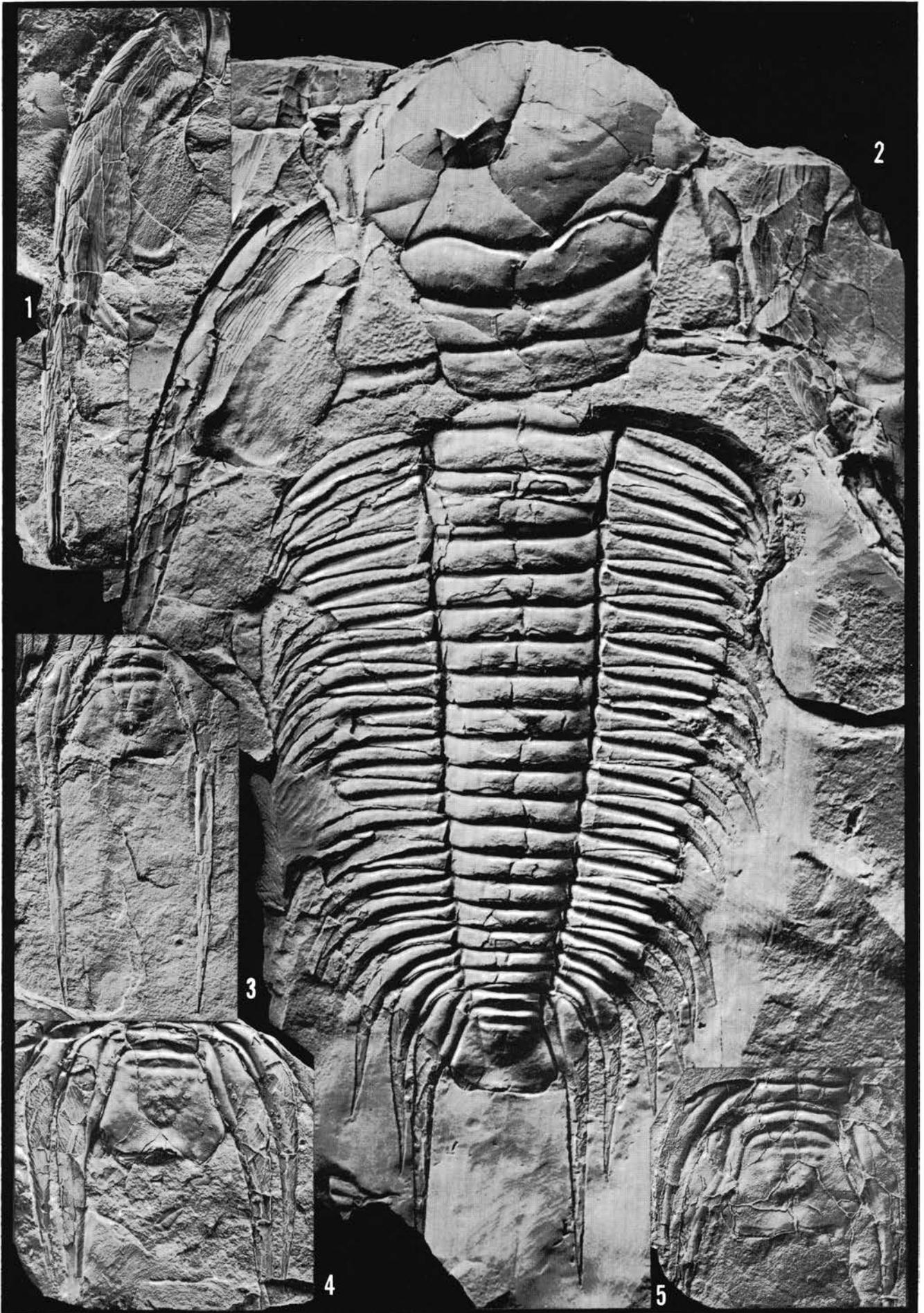


Plate 8

- Fig. 1: *Paradoxides davidis trapezopyge*, from Manuels River, Newfoundland. Cranidium. In addition to the two strong glabellar furrows, two more anterior pairs (S3 and S4) are barely indicated. Section depth 241–256 cm. FMNH PE 25555. 1/1.
- Fig. 2: *Paradoxides forchhammeri* ANGELIN, from *P. forchhammeri* beds at Andrarum, Sweden. Cranidium. Glabellar furrows S3 and S4 strongly developed. Ornament, including terrace lines in the front and tubercles, similar to that in *P. davidis* but more strongly marked. (The ornament is comparatively coarse also in *P. davidis brevispinus*). Occipital node somewhat closer to posterior margin of ring than generally in *P. davidis*. Line running through occipital node probably indicates the position of the margin of the occipital doublure. Gr I 44952. 1/1.
- Fig. 3: *P. davidis trapezopyge* from Manuels. Pygidial region with long spines, which are subparallel behind the pygidium. Part of substantially complete exuviae. Section depth 241–278 cm. FMNH PE 25102 A. 2/1.
- Fig. 4: *P. davidis trapezopyge* from Manuels. Pygidium with fine tubercular ornamentation. Photographic replica from external impression. Section depth 241–278 cm. FMNH PE 25556 B. 2/1.
- Fig. 5 – 6: *P. forchhammeri* from Andrarum, Sweden. Pygidia. As mostly in *P. davidis* only one segmental ring is clearly offset, while others are indicated. Tubercular ornamentation as in *P. davidis* but generally coarser. The posterior indentation and arching reminds very much of *P. davidis*, and as in this species the pygidial doublure is very narrow, as indicated by the marginal band. Photographs from latex casts. LM LO 4878 t and LO 4879 t. 1.5/1.
- Fig. 7: *P. davidis trapezopyge* from Manuels. A rostrum-labral plate indistinguishable from that of *P. d. davidis* (Pl. 5 Fig. 7) and *P. d. brevispinus*. Section depth 241–278 cm. FMNH PE 25109. 1/1.
- Fig. 8: *P. davidis trapezopyge* from Manuels. Portion of thorax to show ornamentation, which is similar to that of *P. d. davidis*. Photographic replica from external impression. Section depth 241–278 cm. FMNH PE 25101 B. 1.5/1.

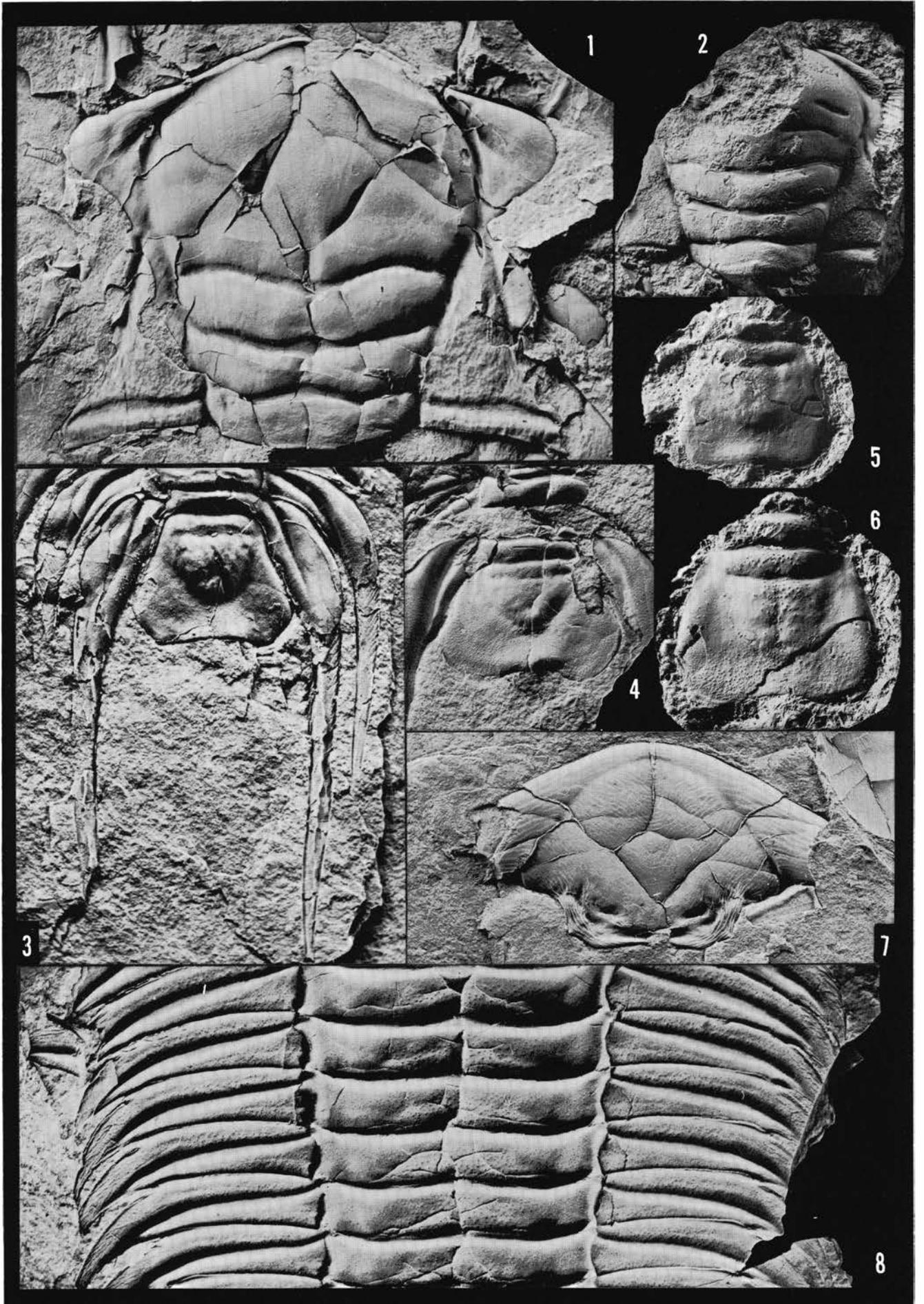


Plate 9

Fig. 1–3: *Paradoxides davidis trapezopyge* from Manuels, Newfoundland. Section depth 241–278 cm. Photographs of a pathological individual.

Fig. 1: Detail of the gross pleural malformation exhibited by specimen in Fig. 3. Photographic replica from external impression. FMNH PE 25557 B. 1.5/1.

Fig. 2: Detail of the pygidial region of specimen in Fig. 3, as seen from external impression. (Photographic replica). FMNH PE 25557 B. 1/1.

Fig. 3: Substantially complete exuviae of pathological individual. Left free cheek displaced. Anterior part of glabella crushed and exfoliated, showing underlying labral plate. Deformities involve fusion of tergites 1 and 2, anomalous number of tergites (18 counting the double tergite as two distinct ones), gross malformations affecting right pleura of tergites 7–11, atrophic left pleural spine in third to last tergite, and irregular termination of right pleura in last thoracic tergite. In addition one may notice that the outline of the pygidium is approaching that of *P. forchhammeri* (cf. Pl. 8, Fig. 5, 6) and that the pygidial rhachis shows unusually distinct segmentation beyond the first axial ring. FMNH PE 25557 A. 1/1.

Fig. 4: *Paradoxides jemtlandicus* WIMAN, 1903, collected by J. C. Moberg in 1908 from *Eccaparadoxides oelandicus* beds at Brunflo railway station, Jämtland, Sweden. The second thoracic tergite is slightly macropleural as in *P. paradoxissimus*. The pygidial morphology may be primitive for the genus *Paradoxides*. Photographed from latex cast. LM LO 4877 t. 2/1.

Fig. 5: *Paradoxides davidis brevispinus* from Manuels River, Newfoundland. Complete thoracopygon with 21 thoracic segments. The pleural spines are short, pointed, with indented posterior margin. Section depth 155–175 cm. FMNH PR 25132 A. 1/1.



Plate 10

Paradoxides davidis brevispinus from Manuels River, Newfoundland.
All specimen from section depth 155–175 cm, 1/1 except Fig. 7.

Fig. 1: Pygidial region. Pygidium and last thoracic tergite indistinguishable from *P. d. davidis* (except possibly for the ornamentation), but other pleural spines considerably shorter. Photographic replica from external impression. FMNH PE 25558.

Fig. 2: Thoracopygon with 20 thoracic segments, isolated cranium and free cheeks. The shape of the most anterior thoracic pleura proves that the thorax is complete. Note the short pleural spines with indented posterior margin. FMNH PE 25133 A.

Fig. 3: Holotype. Almost complete exuviae, missing the free cheeks. All characters distinguishing this subspecies are well represented in this specimen. The cranium is slightly displaced. There are 21 tergites. The cast preserves the exoskeleton so that the prominent surface ornamentation is particularly distinct. The overall outline of the body is slender and subtriangular, due to short pleural spines. The tapered pygidium and last pair of pleural spines conform with many examples of *P. d. davidis*. FMNH PE 28974.

Fig. 4: Cranium, same as seen in lower left corner of Pl. 9, Fig. 5, Tubercular ornamentation and occipital node visible. FMNH PE 25132 B.

Fig. 5: Anterior portion of small individual, from the same assemblage containing specimens in Fig. 1, 6. FMNH PE 25559.

Fig. 6: Pygidium and fused thoracic tergite, from the same assemblage of exuviae containing specimens in Fig. 1, 5. FMNH PE 25559.

Fig. 7: Portion of thorax to show tubercular ornamentation, which is considerably coarser than in typical specimens of *P. d. trapezopyge* and *P. d. davidis*. Photographic replica from external impression. FMNH PE 25132 B. 2.5/1.

