THE TAXONOMY OF SOME UPPER DEVONIAN PHACOPID TRILOBITES FROM SOUTH DEVONSHIRE

by

Mohd. Shafeea bin Leman

Thesis submitted for the degree
of
Master of Science
in the
University of Glasgow
January 1983

I

CONTENTS

CHAPTER 1: INTRODUCTION

CHAPTER 2: SYSTEMATICS

LIST OF TABLES

Note: "—f" indicates the foldout on the following page from the marked page.

LIST OF TEXT-FIGURES

LIST OF PLATES

ACKNOWLEDGMENTS

This research was carried out in the Department of Geology, University of Glasgow, during the tenure of a Malaysian Government (UKM-JPA) scholarship which is gratefully acknowledged.

I would like to thank very much Dr. C.J. Burton for his supervision, advice and discussions throughout the progress of this research and the preparation of this thesis, and also for his permission to use his phacopid collection in this research.

I would like to thank Dr. W. Struve and Miss Dorner for their permission to examine the R. & E. Richter collections in the Senckenberg Museum, Frankfurt, and for their help during my stay in Frankfurt.

Mr. M. Dorling is acknowledged for allowing free access to the Sedgwick Museum Collections. Dr. D. Butler is gratefully acknowledged for allowing free access to the I.G.S. collections, for the loan of some of those collections and for permission to use the materials in my thesis. I would also like to acknowledge Mr White and Dr. E.B. Selwood for the loan of specimens from the Bristol University collections.

Dr. A.J. Gooday is acknowledged for identifying some of the ostracods.

I thank all the staff of the Geology Department for their understanding, help, comments and encouragement.

Thanks to Mr. D. McLean for the photography, Mr. R. M. Morrison for the equipment and the members of Room 220 for their full understanding.

I wish to thank Mr. J.R. Beerman and Mr. Z. Ok for the translations of some German and Russian material.

The owners of Lounston Farm, Combe Farm, Langmead Farm and Rora House are also thanked for allowing access to their land for fieldwork purposes.

Thanks also to the typist Mrs. B. Mackenzie for her tolerance and hard work.

Finally, I would like to thank my parents, family and those who have given me every sort of encouragement.

DECLARATION

The material presented in this thesis summarizes the results of research carried out between October 1980 and December 1982 in the Department of Geology, University of Glasgow, under the supervision of Dr. C.J. Burton. This dissertation is based on my own independent research and any published or unpublished materials used in it have been given full acknowledgment in the text.

Mohd. Shafeea bin Leman

ABSTRACT

This thesis embodies research into trilobites of the family Phacopidae from a number of localities within the Rora Slate and its equivalents of the late Upper Devonian of South-west England. 11 phacopid species including 1 new species, 3 new subspecies, 3 uncertain new species and 1 uncertain new subspecies have been described. They are *Phacops* (*Omegops*) sp. B, *Phacops granulatus* (Münster), *Phacops wedekindi occidentalis* n.ssp., *Phacops wedekindi microps* n.ssp., *Phacops wedekindi* ssp. A, *Cryphops*? *wocklumeriae lounstonensis* n.ssp., *Cryphops*? *ensae* (R. & E. Richter), *Cryphops* sp. A, *Dianops limbatus* (Reinh. Richter), *Dianops griffithides griffithides* (R. & E. Richter), *Dianops tripartitus* (Thomas), *Dianops combensis* n.sp. and *Dianops* sp. A. Among the new features noted in these phacopids are, the spine like mesial tubercle of *Phacops wedekindi occidentalis*, the functional facial sutures of *Cryphops*? *wocklumeriae lounstonensis* and *Dianops tripartitus*, the secondary eyes of *Dianops tripartitus* and the transitory pygidium of *Dianops* sp. indet.. Juveniles of *Phacops wedekindi occidentalis*, *Cryphops*? *wocklumeriae lounstonensis*, *Dianops griffithides griffithides*, *Dianops tripartitus* and *Dianops* sp. indet., some new to palaeontology, have also been described.

These phacopids were found together with proetids, clymenids, ostracods, brachiopods, solitary corals, bivalves, crinoids and bryozoans in the Rora Slate of the Upper Devonian. The two main fossiliferous localities studied, the Lounston fossil band and the Combe fossil band may be referred respectively to the *sphaeroides* subzone and *euryomphala* Zone of the upper Famennian. The Rora

Slate has been correlated with other horizons in South-west England and continental Europe and the biostratigraphy of the British upper Famennian phacopids has been placed in its wider context thereby.

Palaeoecologically the faunas studied herein belong to biocoenosis. The abundance and diversity of the faunas and the type of phacopids they possess indicate that the Combe fossil band was deposited in a deeper environment with a lower nutrient level compared to the Lounston fossil band and also show that the latter was deposited during the late Famennian transgression.

Palaeogeographically, the Rora Slate was deposited on a drowned outer shelf and finally the phacopid palaeobiogeography shows a very close relationship between the spreading of these last phacopids and the change of the sea level. The studied phacopid faunas marked the western limit of the phacopid Realm at that time and the top limit of the family Phacopidae.

CHAPTER 1

INTRODUCTION

1.1 Introduction and aims

Complete successions in the marine facies of the Upper Devonian are known in 3 major areas in SW England. These areas are N Devon, N Cornwall and S Devon. The successions in these areas cannot easily be correlated one with another due to the structural complexity and broken up nature of the area. Fossils, which in some places are numerous, seem to be very valuable in correlating these marine Upper Devonian rocks and also in assigning their component units to the correct places in the succession. The Lounston and Combe fossil bands in the Rora Slate within the Liverton-Ilsington-Bickington succession (see text-figure 1.1, p.5) of S Devon are among those fossiliferous locations, the fossil contents of which are crucial for this process. The phacopid trilobites are among the more important fossils found in these fossil bands. Furthermore the distributions of the faunas in the German type area are very important as reference points for the above-mentioned correlation of the Upper Devonian here (SW England).

Isolated trilobites belonging to the family Phacopidae have, over many years, been found in these beds and several other localities in SW England. These trilobites have been referred to the German types, and where these types have failed to provide a convenient specific designation, a local species has been erected.

The aim of this research is to review the late Devonian deep water members of the family Phacopidae of Britain within the context of

European members of the family. A large, new and well-localized collection together with museum materials provides good data for this purpose. The majority of these phacopids can be compared with one another and the resultant specific and generic groupings compared with those erected by R. & E. Richter in Germany. In this way the rich fauna of the Rora Slate (including the Lounston and Combe fossil bands and several other localities around them) can be used as a foundation in organising the present piecemeal knowledge on a more complete and rational basis. A knowledge of palaeoecology, palaeobiogeography and stratigraphy of the area may also be derived from the study of the phacopids and other members of the fauna.

1. 2 Previous research

The first recorded mention of phacopid trilobites from the Rora Slate is found in the work of Ussher (1913). Ussher found 2 phacopid locations in the Rora Slate and in his publication noted that:

i) ... "in an exposure of greenish grey and buff slates at a by-lane by the road 6½ furlongs (= 1.1km) West of Liverton (where) I noticed the occurrence of numerous Clymenia

> Clymenia undulata (Münster)
> Orthoceras sp.
> ?Phacops (Trimerocephalus) sp.

These beds may be overlain by the representative of the Lower Culm chert-beds on the North, but on the East they are faulted against the Lower Culm"------p.39.

ii) ... "and greenish-grey slates are visible by the road which forms the western boundary of Ramshorn Down. They furnished the following fossils :-

Cladochonus?
Orthis sp.
Posidonia venusta (Münster)
Entomis?
Phacops (Trimerocephalus?) sp. (thorax and pygidium)"
------p.40

The first location corresponds to the Lounston fossil band of the present study, while the second location cannot be fixed with certainty. It could correspond to the Combe fossil band or locality 7 of Waters (the I.G.S. mapper who collected some fossils from the Rora Slate in 1971).

In 1968, Selwood and Burton mentioned the presence of proetids as well as dimorphic phacopids in the Lounston fossil band. During this research Burton also collected some phacopids which, according to him (personal communication), are closely similar to those of Germany.

In 1971, Waters made a large collection of fossils from almost every fossiliferous location within the exposed Rora Slate; this collection including a large number of phacopid trilobites. These big, well localized but unclassified collections were presented by the collector to the Institute of Geological Sciences (I.G.S.)Museum. The phacopid trilobites from Waters' collection have been classified as part of the present research.

Outside the Rora Slate, late Devonian phacopids are also known from the Chudleigh area, recorded by Roemer (1880), Ussher (1890), Thomas (1909) and House and Butcher (1973); from Newton Abbot, Ussher (1913); from Viverdon Down, Cornwall, Whiteley (1981); from Launceston, Cornwall Salter (1864), Reid (1911), Selwood (1959, 1960), Edmonds, McKeown and Williams (1975); from the Tavistock area, Dearman and Butcher (1959) and from Barnstaple, N Devon, Goldring (1969).

Thomas (1909) described species from the Whiteway Farm locality, the designations of which were later questioned by R. & E. Richter (1926) and Chlupac (1977[i]). Selwood (1959, 1960) described phacopid trilobites of an equivalent age to those of the Rora Slate from the Stourscombe Beds which represent the Wocklumeria Stufe of the Launceston area. He noted a few variations in his specimens in respect of the German types of his species.

In Germany the major work on the Upper Devonian phacopids by R. & E. Richter (1926) is taken to be the definitive study. Most of the phacopids studied by R. & E. Richter come from the eastern Rheinische Schiefergebirge (including the Apricke and Riemke localities of Iserlohn, the Effenberg, Dasberg and Hönne-Tal localities of Balve, the Langenaubach locality of Dillenburg, Rüthen, Elberfeld, Barmen and several other localities). Other localities include Thuringia (including the Schubelhammer, Saalfeld and Gattendorf localities), the Harz Mountains; as well as from outside Germany. Included in R. & E. Richter's study is a revision of Thomas' Whiteway Farm phacopids. Other systematic descriptions of Upper Devonian phacopids were made by R. & E. Richter in 1933 and 1955 supplementing their earlier work.

Pfeiffer (1954) described the Upper Devonian phacopids from the Bohlen near Saalfeld, Thuringia, most of them being blind phacopids. In 1955 Maksimova described the Upper Devonian phacopids of Russia which come from the Ural Mountains and the northern Mugodjar area and include both blind phacopids and those with well developed eyes. In 1958, Osmolska described the sighted phacopids of the Holy Cross Mountains of Poland and in 1966 and 1977[i] Chlupáč described the phacopid trilobites of

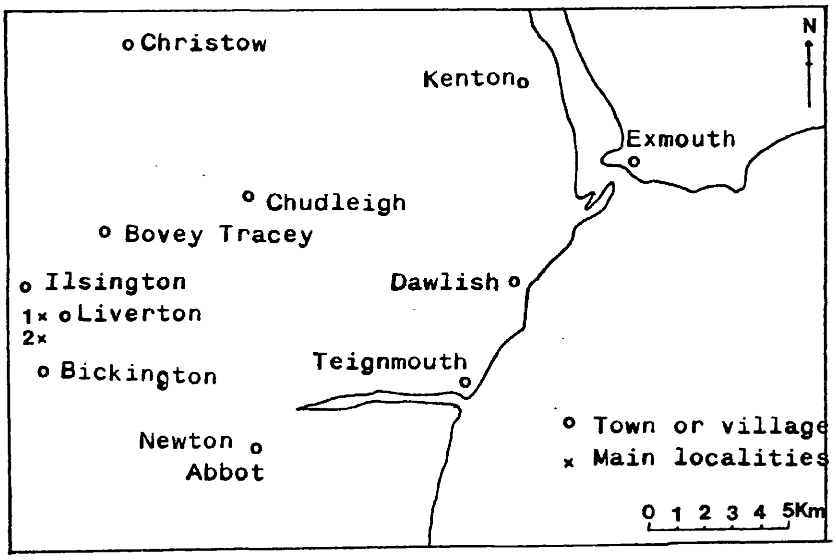
Czechoslovakia, including some late Devonian phacopids from the Hády Limestones. In 1980, Maksimova assembled evidence to suggest that Upper Devonian phacopids could be used as stratigraphical index fossils and produced a list of trilobites to be so used.

Further important work on the Upper Devonian phacopids was done by Struve, firstly in Moore (1959) and then in 1976 in which he reorganized Richter's classification of the phacopids.

1. 3 The Liverton - Bickington - Ilsington area

The key area for the present work is the Liverton - Bickington - Ilsington area which is situated on the eastern flank of the Dartmoor Granite, about 3.5 Km South-West of Bovey Tracey (see text-figure 1. 1 below). This area contains, among other formations, those of the Upper Devonian which are stratigraphically the oldest.

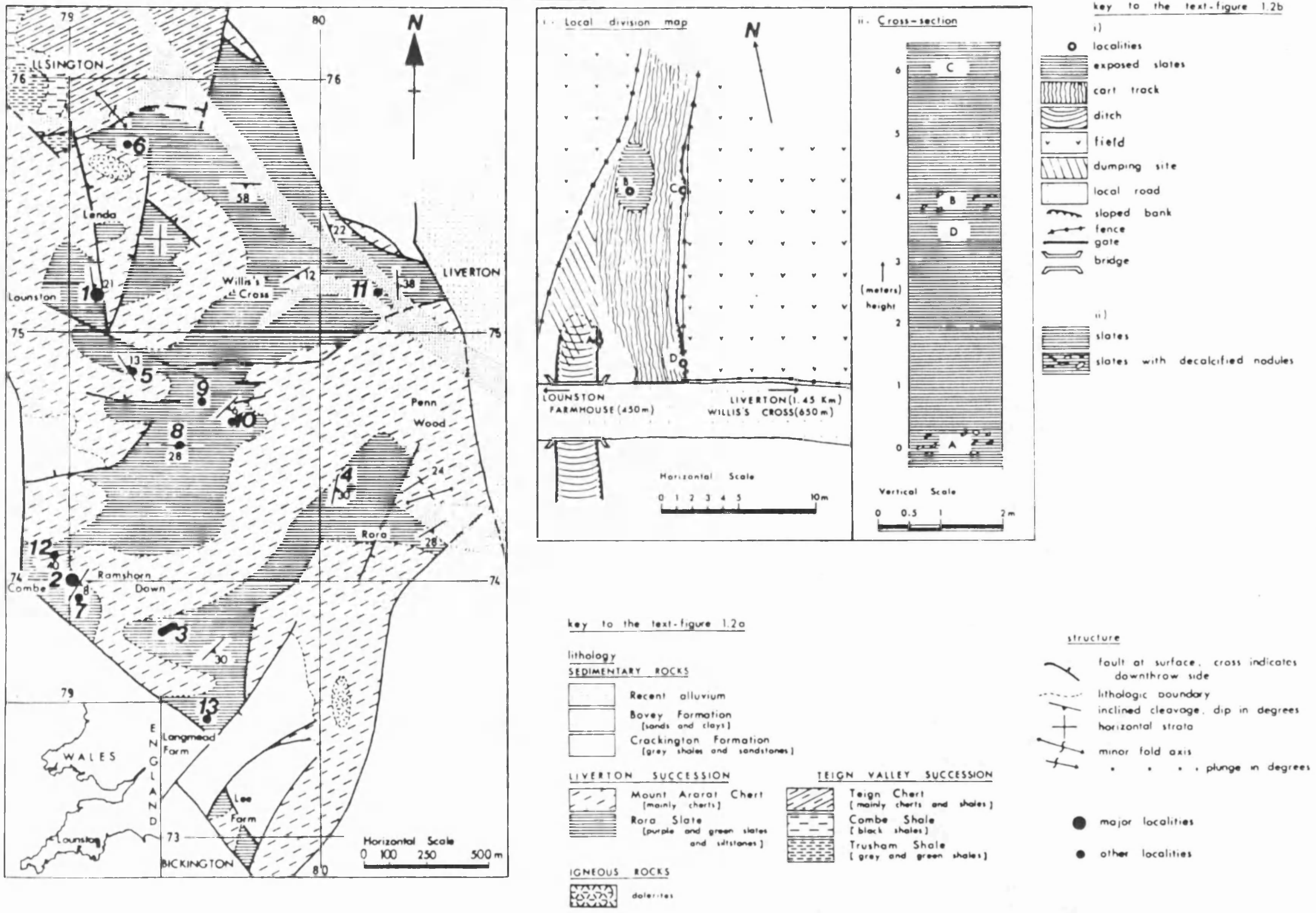
Text-figure 1. 1 : Referrence map for the study area (from Sheet No. 339, I.G.S., 1976).



→ Text-figure 1.2

Text-figure 1.2

a Locality and geological map of the Ilsington-Bickington-Liverton area b Local divisions and vertical cross-section of the locality 1



The local representative of the Upper Devonian is the Rora Slate, the base of which although not visible in this area may, from evidence derived elsewhere, overlie the middle part of Upper Devonian. Those parts of the Rora Slate which are seen can, by their clymenids, ostracods and trilobites be referred to the *Wocklumeria Stufe* (the Lounston fossil band ≡ *sphaeroides* subzone, the Combe fossil band ≡ *euryomphala* zone). The local lateral equivalents of these beds are the Gurrington Slate of Newton Abbot, the Mount Pleasant Series and the Whiteway Slates of Chudleigh, the Stourscombe Beds of N Cornwall and the Lower Pilton Beds of North Devon. Further afield they are equivalent to the "Wocklumer Schichten" and "Hangenberg Schiefer" of the Rheinische Schiefergebirge, the upper part of the*"Ostracod Slates" and "Clymenia Beds" in the Dill/Lahn synclinorium and eastern Thuringia, the Hády Limestone of Czechoslovakia, an unnamed shale in the Holy Cross Mountains of Poland and the Mugodjar limestone of the U.S.S.R.

The Rora Slate is overlain directly by the Mount Ararat Chert of Lower Carboniferous age.

1.3.1 *Lithology and structure* (see text-figure 1.2a, p.5)

The Rora Slate, as it's name implies, consists mainly of slates of various colours, poorly cleaved and in many places strongly jointed. Decalcified and siliceous nodules are locally developed. Thin limestone layers were found by Waters at 2 localities (9 and 10)(see text-figure 1.2a for the position of all fossiliferous locations in the study area).

The structural complexity and the strongly faulted nature of the

* = "Cypridinen Schiefer" and "Clymenia Schichten"

Upper Devonian here not only isolates this area (i.e. the Liverton-Bickington-Ilsington area) from the others in the region, but also separates the area itself into several isolated units. These isolated units can only be correlated by means of fossils.

1. 4 Locations sampled (see text-figures 1a and b, p.5)

The Lounston and Combe fossil bands were studied in more detail than the others because of their high content of phacopid trilobites.

i) The Lounston fossil band (M.R. 79087515) is located about 450m at N78°E from the farmhouse at Lounston Farm. For the purpose of the present study it was divided into 4 localities, i.e. localities 1A, 1B, 1C and 1D (their lateral and vertical relationships are shown in text-figure 1.2b, p.5). All of these localities are made of bluish grey slates, with rare decalcified nodules at localities 1A and 1B. Some of these nodules are fossiliferous but most of the fossils come from the slates themselves. The bedding planes at locality 1A dip at 24° toward N85°E, while at locality 1B they dip at 19° toward N81°E. Apart from the author's collections, fossils from locality 1A are also available in Waters' and Burton's collections. The localities 1B and 1C were found during the progress of this research, while locality 1D was discovered by Waters. Ussher's collection, while coming from the same place, cannot be referred to any of these localities.

ii) The Combe fossil band (M.R. 79057400) is located 1.1km South of the Lounston fossil band on a road cutting facing the local road - main farm track junction, 350m at N363°E from Ramshorn Down and 200m at N108°E from the farmhouse at Combe Farm. This fossil band is made of greenish to yellowish compact slates which are poorly bedded but strongly jointed. The systematic orientation of the less distorted phacopid trilobites show that the bed dips at 8° toward N122°E. This is a new locality for phacopid trilobites.

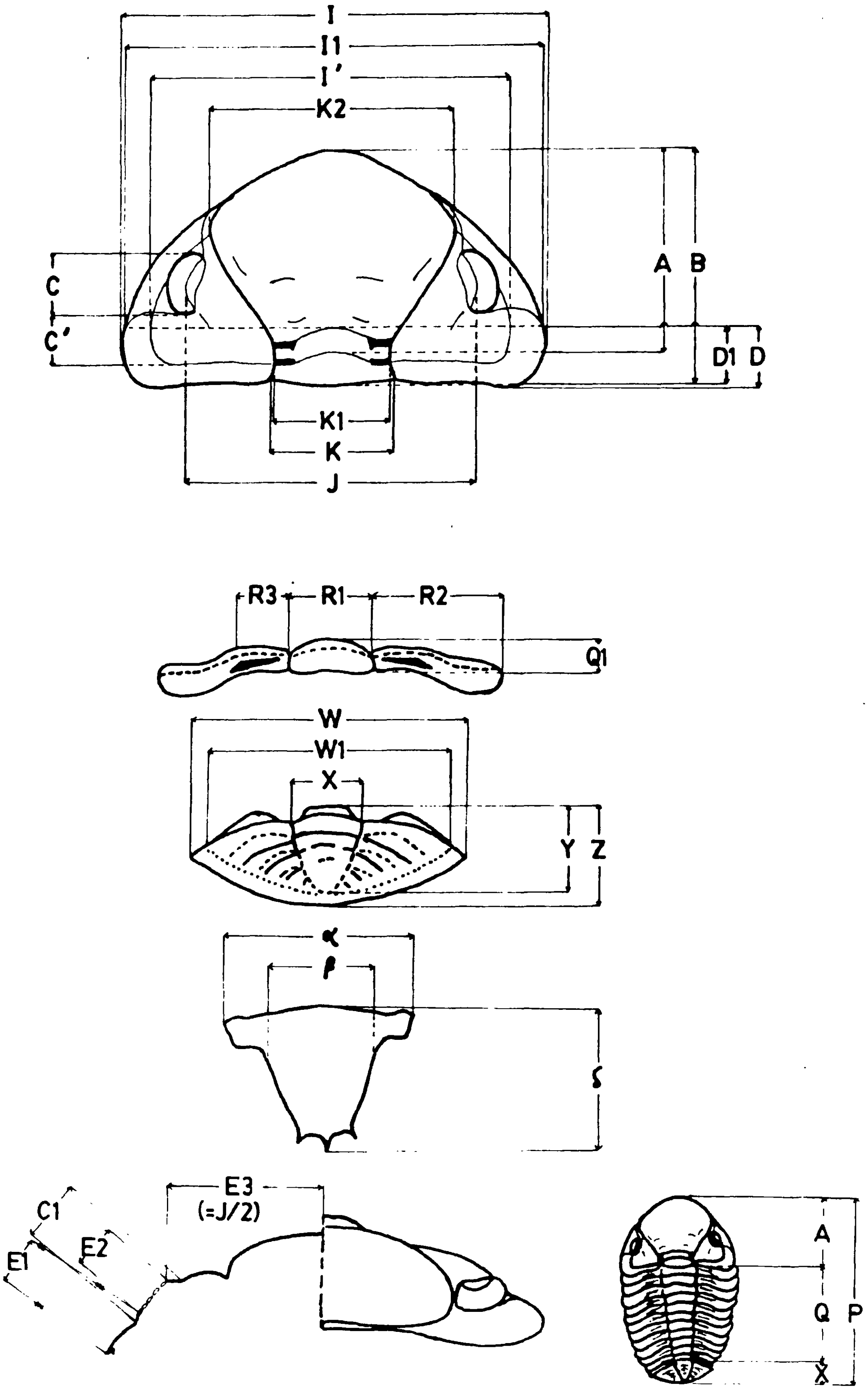
Trilobites are also found in 11 other fossiliferous localities in the Rora Slate, most of them bearing phacopid as well as proetid trilobites. For details on the position of these localities see text-figure 1.2a, p.5f. Localities 3 to 10 are Waters' localities, while 11 to 13 were found during the progress of this research, together with the Lounston and Combe fossil bands.

1. 5 Working methods and early results

In the field the slates were studied systematically and the trilobite bearing slates were sampled. In the laboratory, the complete fauna, including trilobites was extracted by the usual methods i.e. by needles and brushes and, whenever necessary, dental tools. Most of the fossils are thin-shelled and very fragile, being made of the original materials or of iron oxide replacing the original materials. This being so, very careful treatment is needed to release these fossils from their matrix. Latex casts were produced from external moulds for two reasons, firstly because the carapace or the internal mould is missing or, secondly, because the cast from the external mould usually reveals more details than that of the carapace or internal mould.

Each phacopid was studied under the binocular microscope and was classified and described carefully. Whenever finer detail was needed the scanning electron microscope was used to provide the necessary high magnification. The studied phacopids were measured for further statistical work in support of the morpholocial descriptions, or in

→
text-figure 1.3



Text-figure 1.3 Measured parameters for statistics use pursuit of morphological variations within certain species. (see text-figure 1.3, p.8f for details on measured parameters). All phacopids were photographed by using an ordinary SLR camera (adapted with a closeup lens) and some photographs were also produced by the camera attached to the scanning electron microscope.

91kg of rock was taken from locality 1A and from it 64 phacopids and 50 proetids were found, together with brachiopods, bivalves, ostracods, solitary corals and crinoids. These phacopids were classified into 3 genera and 6 species while the proetids come from 4 genera and 6 species.

19kg of rock was taken from locality 1D and from it 2 genera and 4 species of phacopid and 1 single proetid were extracted.

From the Combe fossil band (locality 2), from 84kg of rock taken only 1 species of phacopid and 4 pieces (? 1 species) of proetid were collected. However more than 80 individuals of the single phacopid species were isolated. The rest of the fauna from this locality is sparse.

For further details on the number as well as the type of phacopid found at every locality studied see table 4.2, p.119f. Details on the complete faunas, regardless of their number of occurrences, can be seen in table 3.2, p.110f.

1. 6 Classification, comparison and the Museum collections

After the local phacopid collections (including those of Waters, Burton and Ussher) were classified, they were compared with the established faunas elsewhere in Britain. This stage being completed, work then began on the comparison of total British fauna with those of Continental Europe.

Both Waters' and Ussher's collections were borrowed from the Institute of Geological Sciences (I.G.S.) Museum, London, while Burton's collection was available from the Department of Geology, University of Glasgow.

For comparison the Chudleigh material, which is stored in the Sedgwick Museum, Cambridge, was studied. These specimens were classified by Selwood in House and Butcher (1973).

Bristol University houses large collections of phacopid trilobites which were borrowed for detailed study. These collections come from the Launceston area of Cornwall and, like the Chudleigh materials, these specimens were also identified and classified by Selwood (see Selwood, 1960).

Beside the British phacopids, the German species in the Senckenberg Museum, Frankfurt, collected by R. & E. Richter were also examined. Among these collections are included some type species described by R. & E. Richter in 1926. Although the collections are quite small, they are very well preserved and the status of their species is beyond doubt.

Comparisons having been made between the British and foreign (especially German) collections, the systematic positions of the British specimens were revised. This and the data furnished by the foreign material enabled work to be done upon the palaeoecology, biostratigraphy and palaeogeography of the Upper Devonian phacopids in Britain and Europe.

CHAPTER 2

SYSTEMATICS

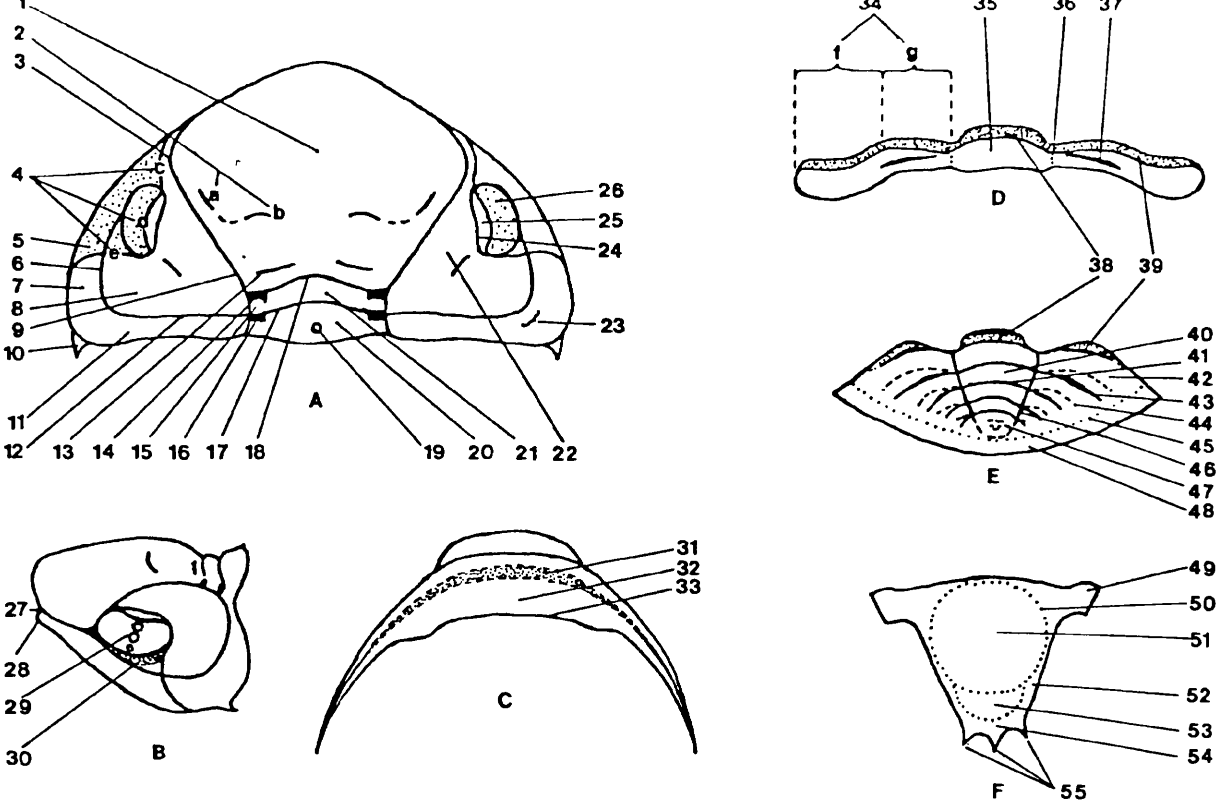
2. 1 Introduction

From all the collections of the phacopid trilobites from the study area, including those of the present author and those of Waters and Burton, 3 genera and 1 subgenus have been identified. They are *Phacops* Emmrich including subgenus *Ph.* (*Omegops*) Struve, *Cryphops* (R. & E. Richter) and *Dianops* (R. & E. Richter). The genus *Phacops* includes *Ph. granulatus* (Münster), *Ph. wedekindi occidentalis* n.ssp., *Ph. wedekindi microps* n.ssp. and *Ph. wedekindi* ssp. A, while the subgenus *Ph.* (*Omegops*) is represented by *Ph.* (*Om.*) sp. B. The genus *Cryphops* includes *Cr.*? *wocklumeriae lounstonensis* n.ssp., *Cr.*? *ensae* R. & E. Richter and *Cr.* sp. A. Finally the genus *Dianops* is represented by *D. combensis* n.sp., *D. tripartitus* (Thomas), *D. griffithides griffithides* (R. & E. Richter), *D. limbatus* (Rheinhard Richter) and *D.* sp. A.

Also found were juveniles from *Ph. wedekindi occidentalis* n.ssp., *Ph.* sp. indet., *Cr.*? *wocklumeriae lounstonensis* n.ssp., *D. griffithides griffithides*, *D. tripartitus* and *D.* sp. indet. All of them are meraspids, probably a later stage in meraspis.

Some localities yielded numerous proetids which are far better preserved than the phacopids. These proetids mainly come from the genus *Typhloproetus* Rud. Richter (includes *T. subcarintiacus* Rud. Richter and *T.* ?*microdiscus* Rud. Richter) and *Chaunoproetus* R. & E. Richter (includes *Ch. palensis* (Rud. Richter) and *Ch. tietzei* R. & E. Richter) and a few came from the genus *Drevermannia* Rud. Richter (*Dr.*

→
Text-figure 2.1



Text-figure 2.1 : Morphological terms used in text.

A= Cephalon, top (plan) view.
1=Frontal glabellar lobe
2=S3 glabellar furrow
  a. anterior ramus
  b. posterior ramus
3=Lateral glabellar corner
4=Facial suture
  c. preocular branch
  d. ocular branch
  e. postocular branch
5=Librigena
6=Lateral border furrow
7=Lateral border
8=Postocular genal field
9=Axial furrow
10=Genal spine
11=Posterior border
12=Posterior border furrow
13=S2 glabellar furrow
14=Lateral preoccipital pit
15=Lateral preoccipital lobe
16=Lateral occipital pit
17=Occipital furrow
18=S1 preoccipital glabellar furrow
19=Mesial tubercle
20=Occipital ring
21=Preoccipital ring
22=Palpebral eye stem
23=Genal angle
24=Palpebral furrow
25=Palpebral lobe
26=Visual surface

B= Cephalon, side view
27=Anterior border furrow
28=Anterior border
29=Dorsoventral files of lenses
30=Eye socle

C= Cephalon, front view
31=Vincular furrow
32=Anterior doublure
33=Hypostomal suture

D= Thorax
34=Pleura
  f. outer half
  g. inner half
35=Axial ring
36=Axial furrow
37=Pleural furrow
38=Anterior half ring
39=Anterior half pleura

E= Pygidium
40=Axial ring
41=Ring furrow
42=Pleura
43=Pleural furrow
44=Interpleural furrow
45=Border furrow
46=Axial furrow
47=Terminal piece
48=Border region

F= Hypostome
49=Anterior wing
50=Border furrow
51=Anterior lobe
52=Lateral border
53=Posterior lobe
54=Posterior border
55=Denticles

?schmidti (Rud. Richter). Sighted cyrtosymbolinids are very rarely found.

note:

i) All the descriptions are based on the actual carapace unless otherwise stated. The morphological terminology used is taken mainly from the Treatise on Invertebrate Paleontology, Volume O(1) edited by Moore (1959). Some further supplementary additions are taken from various other papers. These morphological terms are well summarised and can be seen in text-figure 2.1, p. 11f.

ii) "Zo..." (LC) - Present author's collection (major part). Lodged in the Institute of Geological Sciences (I.G.S.) Museum, London.

"Zo..." (BC) - Burton's collection lodged in the I.G.S. Museum, London.

"HMA..." - Present author's collection (in part) lodged in the Hunterian Museum, University of Glasgow.

"AD..." (WC) - Waters' collection lodged in the I.G.S. Museum, London.

2.2 Systematics

Phylum: ARTHROPODA
Family: PHACOPIDAE Hawle and Corda, 1847
Genus: Phacops Emmrich, 1839

2.2.1 Phacops granulatus (Münster, 1840)

(Plate 1, figures 1-7, text-figure 2.4a, p.28f).

1864 Ph. (Phacops) granulatus (Münster); Salter p.18 pl. 1, figs. 1-4.

1913 Phacops granulatus (Münster); Paeckelman pp.172-173.

1926 Ph. (Phacops) granulatus (Münster); R. & E. Richter, pp.137-142, pl.8, figs.34-39, text-figs. 17b, c.

1955 *Phacops granulatus* (Münster); Maksimova, pp. 136-140, pl.10, figs. 3-11.

1958 *Phacops granulatus* (Münster); Osmolska, pp. 125-127, pl.10, fig. 1, text-fig. 2.

1966 *Ph.* (*Phacops*) *granulatus* (Münster); Chlupáč, pp. 104-105, pl. 22, figs. 4-10.

1969 *Phacops granulatus* (Münster); Selwood and Burton, pp. 197, 199.

1975 *Phacops granulatus* (Münster); G. & R. Hahn, p. 21, pl. 2, fig. 6.

1977 *Ph.* (*Phacops*) *granulatus* (Münster); Chlupáč, pp. 45-46.

Localities: Localities 1A, 1D and 3 (see text-figure 1.2, p.5f).

Horizons: The Rora Slate - Zone Vβ to VIβ of the Fammenian - the localities 1A and 1B fall into Zone VIβ (= *sphaeroides* subzone), while the exact age of the locality 3 is uncertain.

Materials: 10 specimens from locality 1A and 1 specimen from each of the localities 1A and 1D.

From Locality 1A: Specimens Nos. Zo 4529, 4533-4537 (LC), Zo 4538-4540 (BC).
From Locality 10: Specimen No. AD 1896/7 (WC).
From Locality 3: Specimen No. AD 1124(WC).

Preservation: Generally the condition of preservation is not very good.

Diagnosis

Cephalic outline almost semicircular with well rounded genal angle. Glabella inflated, strongly expanding forward, its posterolateral margin almost straight. Glabella angle narrow (65°-70°). S2 and S3 glabellar furrows are absent. Preoccipital ring quite well defined. Axial furrow wide and deep. Facial suture obsolete. Eye medium to large with 31 to 38 lenses. Palpebral furrow abaxially curved. Eye socle narrow. Lateral border furrow continuous at the eye base. Anterior glabellar margin overhanging slightly. Anterior doblure narrow. Vincular furrow deep, wide medially and narrow laterally. Surface of the cephalon heavily granulated except on the border.

Description

Small trilobites with sagittal cephalic lengths from 3.8mm to 5.8mm, with the maximum cephalic width nearly twice the length. The cephalic outline less the posterior margin is roughly semicircular. The anterior margin of the cephalon is smoothly curved and the genal angles are smoothly rounded and parabolic. The posterior cephalic margin less the occipital ring is weakly curved forward. In front view, the glabella is strongly convex; the genae are also convex separated from the lateral borders by at least a shallow border furrow. In side view the glabella is quite strongly inflated, tallest at the rear end of the frontal glabellar lobe, sloping weakly forward to the thick and overhanging anterior glabellar margin. The anterior border furrow is shallow but well-marked. The anterior border is swollen. Rearward of its summit, the glabella drops down sharply to the preoccipital ring which is low and unobtrusive. The occipital ring is obtrusive.

The glabella is inflated and expands quite strongly forward. The glabellar angle ranges from 65° to 70°. The posterolateral glabellar margins are almost straight so that the glabellar angle remains constant from its entrant angle to the lateral glabellar corner. The lateral glabellar corner is short and slightly angular. The anterior glabellar margin is smoothly curved forward. There are no S_2 and S_3 glabellar furrows. The S_1 preoccipital glabellar furrow is shallow and narrow but continuous and curved forward medially. The lateral preoccipital pits are deep and laterally elongated but very short. The preoccipital ring is quite well marked. It is short, narrow, low and unobtrusive. The median and lateral preoccipital lobes are separated by a shallow depression. The median preoccipital lobe has a planoconvex or a slightly crescentic outline. The lateral preoccipital lobes are small, rounded to square in outline. The occipital furrow is shallow and narrow, very weakly curved forward or straight medially. The lateral occipital pits are deep and laterally elongated, usually shorter transversely than the lateral preoccipital pits. The occipital ring is short, narrow, obtrusive and usually has a planoconvex or slightly biconvex outline.

The axial furrows are wide and deep. The genae are small and inflated, with their anterolateral corners occupied by the eye. Most of the genal field consists of the fixigenae which are themselves faintly divided by a shallow depression into the palpebral eye stems and the postocular genal fields. Most parts of the librigenae are restricted to the border area. The fixigenae and librigenae are divided posteriorly by the traces of the facial sutures; anteriorly they are inseparable. The facial sutures are non-functional. Their postocular branches appear at the rear end of the visual surfaces, smoothly curved in anterolateral direction and terminated at the lateral cephalic margins shortly in front of the genal angles. The genal fields are separated from the border areas by the narrow and shallow border furrows. The posterior borders are narrow adaxially, widening toward the genal angle where they meet the lateral borders.

The lateral borders, widest at the genal angle, narrow gradually forward to the anterior borders. The posterior borders are more swollen than the lateral borders. The anterior borders are wide and flattened laterally and narrow and swollen medially. The anterior border furrow is narrow and shallow but continuous medially. The anterior doublure is narrow and crescentic in shape. The vincular furrow is deep, wider medially, narrowing laterally, continuous along the lateral cephalic margin and terminated at the genal angle. The doublure behind the vincular furrow is slightly swollen.

The eyes are medium to large in size, their length being slightly longer than 1/3 of the cephalic length. The eyes are kidney-shaped in outline. The palpebral furrows are narrow and shallow, abaxially curved medially, while anteriorly they meet the axial furrows forming cusps between them. The anterior parts of the eyes are bounded by the axial furrows. The palpebral lobes are weakly swollen, widest medially where they curve abaxially, and narrowing toward both posterior and anterior ends. The eye socles are narrow, wider posteriorly and narrowing forward. Sometimes the anterior parts of the eye socles are so narrow that the visual surfaces seem to rest completely on the genae. The baseline of the eyes does not interrupt the border furrows and usually coincides with them at least in their anterior half, their posterior ends being considerably elevated. The visual surfaces are long and wide, steeply sloping and asymmetrically kidney-shaped. The top outlines of the visual surfaces are smooth while the bottom outlines are irregular and consist of the boundary between the eye socles and the scleral rims of the bottom row lenses. The visual surfaces contain 31-38 lenses each of which is of small (diameter up up to 0.25mm), rounded and biconvex, and set in a hexagonal rim of sclera. These lenses are arranged in 13 dorsoventral rows with a maximum of 4 lenses in the longest row. The front dorsoventral rows are longer than the back rows. The even dorsoventral rows are longer than the odd ones in the front half of the visual surface though sometimes the rows become irregular and lose definition. The back 4 rows seem to be very uniform in all the specimens. Except for the small top lenses of a few middle dorsoventral rows, the other lenses generally increase in size from bottom to top.

The surface of the cephalon is heavily granulated. On the external mould and carapace small hemispherical granules with diameters of 0.2mm or less are irregularly and densely distributed over almost all the cephalon except on the border region where finer granules with diameters of around 0.05mm are scattered more sparsely than on the other parts. On the anterior border ridge there is one row of granules of smaller size than the granules elsewhere on the cephalon. The mesial tubercle is absent.

Comparison and discussion

In general morphology the Liverton specimens (i.e. the Lounston and Ramshorn Down specimens) are closely similar to the specimens of *Phacops granulatus* from elsewhere in Britain and in Europe. However a detailed comparison has revealed some small differences. The comparison between the Liverton specimens and the other specimens of this species elsewhere can be discussed more easily in the context of dimorphism, than if they are discussed individually.

Remarks on dimorphism

From the present study which covers all the Liverton and

Launceston specimens and some of the German specimens, together with published data from the German and Polish specimens, 2 possibly dimorphic groups can be found in this species, i.e. Ph. granulatus. This dimorphic classification differs from that of Selwood & Burton (1969) in being based mainly on the features and growth patterns of the eye whereas Selwood & Burton's dimorphic classification is based on the granulation pattern of the carapace and the features of the preoccipital ring. Furthermore the present suggested dimorphism is not restricted to local populations like that of Selwood and Burton which is found in the Launceston specimens only. The present suggested dimorphism can be found in the Launceston, and the German and Polish specimens but is not very obvious in the Liverton specimens. The reason is that the specimens found here are small in size and that this dimorphism is less obvious in the smaller adult specimens than it is in the larger ones (see text-figure 2.2b, c, p. 19f). Dimorphism of this kind (i.e. clearer in the larger adult than in the smaller one) is the norm within the Arthropoda, sexually dimorphic characteristics being produced only in the adult stage. The differences between these 2 dimorphic groups, namely Group A and Group B are summarized in the table 2.1, p. 19.

All the Liverton specimens are close to dimorph B. The absence of the dimorph A in this area is not fully understood but most probably because of lack of data especially on the larger specimens.

Table 2.1 Dimorphism in *Phacops granulatus* (Münster, 1840)

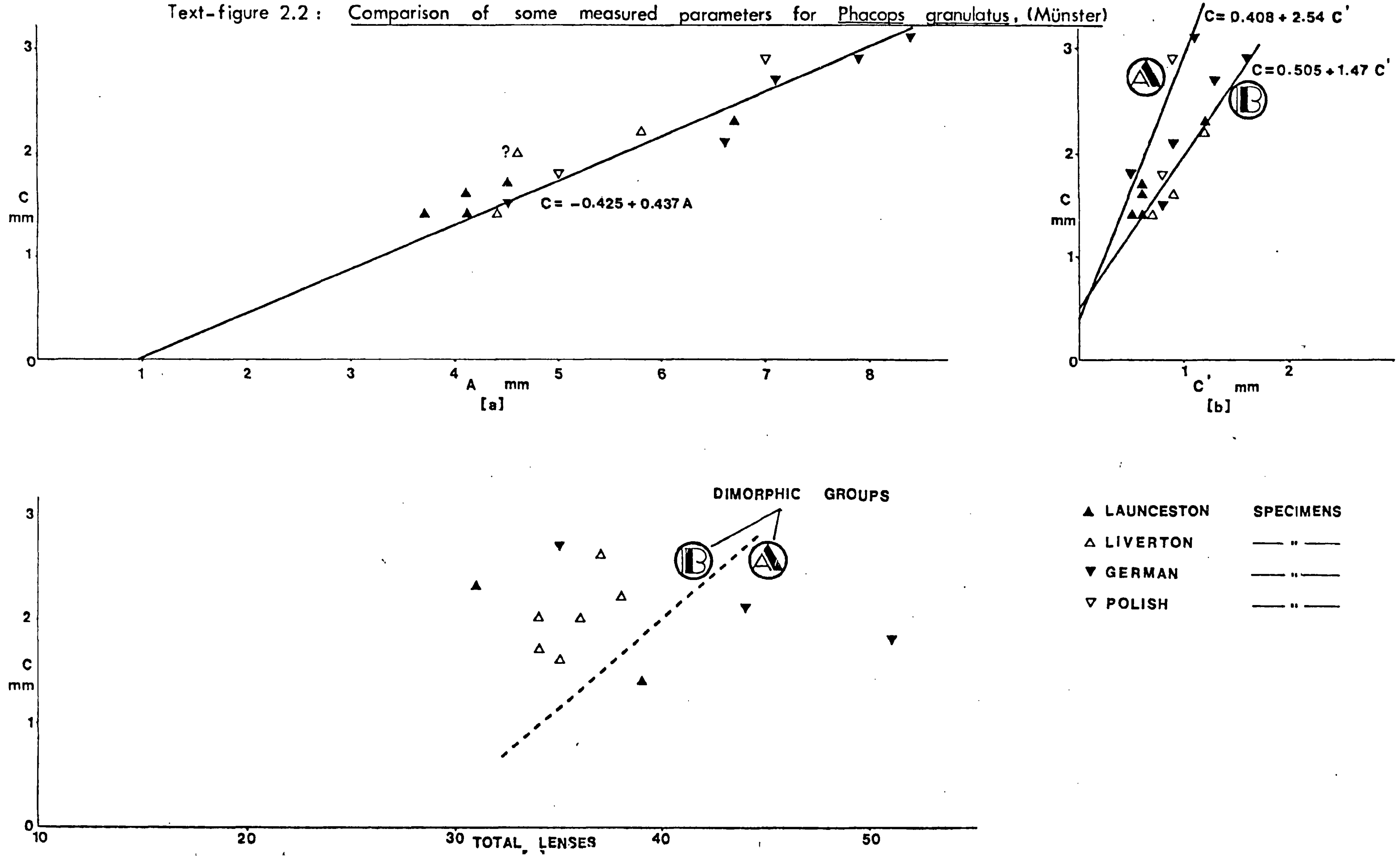
Dimorph A	Dimorph B
1. For a given eye length the total number of lenses is bigger than in Dimorph B.	1. Vice versa
2. The lenses are small and closely packed.	2. The lenses are bigger than in Dimorph A and quite loosely packed.
3. The maximum number of lenses per dorsoventral row usually reaches 5.	3. The maximum number of lenses per dorsoventral file is 3 or 4.
4. The post-ocular genal fields are very small. ($C = 0.408 + 2.54C'$).	4. The post-ocular genal fields are wider than in Dimorph A. ($C = 0.505 + 1.47C'$).
5. The palpebral furrows are more strongly abaxially curved than in Dimorph B.	5. Vice versa

Because the granulation is missing in most of the Liverton specimens the present author is unable to demonstrate Selwood's dimorphic classification based on this criterion. However the generally poorly developed preoccipital ring in all the Liverton specimens suggests that the Liverton specimens belong to the form Y of Selwood and Burton. Form X of Selwood & Burton seems to be absent in the study area.

The closest related phacopids are *Ph. wedekindi wedekindi* R. & E. Richter and *Ph. wedekindi uralicus* Maksimova which resemble the Liverton *Ph. granulatus* in having a similar number of dorsoventral rows of lenses and similar ranges of C:A and C:C' ratios

→ text-figure 2.2

Text-figure 2.2 : Comparison of some measured parameters for *Phacops granulatus*, (Münster)



(see text-figure 1.3 for abbreviations) and total number of lenses (see text-figures 2.2 and 2.3). However *Ph. wedekindi wedekindi* and *Ph. wedekindi uralicus* can be distinguished from the Liverton *Ph. granulatus* by having adaxially curved palpebral furrows, interrupted lateral border furrows at the eyes, shallower axial furrows and a more poorly developed preoccipital ring.

2.2.2. *Phacops wedekindi microps* subsp. nov.

(Plate 2, figures 1-5, text-figure 2.4c, p.28f).

1926 *Ph.* (*Phacops*) *wedekindi* R. & E. Richter; R. & E. Richter (*partim*), pp. 145-147, pl.8, figs. ?42, 43.

? 1958 *Phacops wedekindi wedekindi* R. & E. Richter; Osmolska, pp. 127-128, pl.1, figs. 2a, b.

1960 *Ph.* (*Phacops*) *wedekindi* R. & E. Richter, Selwood, p.177.

Deriv. nom.: From "microps" - latin for "small eye"; this subspecies has the smallest eye among the subspecies of *Ph. wedekindi sensu lato* R. & E. Richter.

Holotype: BU 12930a,b (Selwood's collection in the Department of Geology, Bristol University); this specimen is the biggest among Selwood's collection (incl. BU 12930-12932). The holotype is better preserved than the German member of this subspecies, Rx 574e (R. & E. Richter's collection in the Senckenberg Museum, Frankfurt, in having its original carapace preserved. Compared to the Lounston specimen (incl. LC, BC and WC) the holotype is better because it has retained its original curvature. Lack of eye details in the holotype and other specimens from Germany and Cornwall, require some paratypes to diagnose this subspecies.

Paratype I: Zo 4558a, b (LC) shows the eye orientation

Paratype II: Zo 4559 (LC)

Localities: Localities 1A, 1C and 1D of the Lounston fossil band (see text-figure 1.2b, p. 5).

Horizons: The Rora Slate, Zone VIβ of the Famennian (≡ sphaeroides subzone).

Materials: From locality 1A - specimens nos. Zo 4558-4572 (LC), Zo 4573-4575 (BC), HMA 21152 (LC).

From locality 1C - specimens nos. Zo 4673-4674 (LC).

From locality 1D - specimen no. AD 1896 (WC).

Conditions: In general the condition of preservation is not very good.

Diagnosis

Cephalic outline slightly longer than semicircular with well rounded and parabolic genal angles. Glabella inflated, expanded strongly forward with almost straight posterolateral margins. Glabellar angle wide. Lateral glabellar corners slightly angular. Preoccipital ring well defined with well developed lateral preoccipital lobes. The eyes have a circular outline with narrow, weakly sloping and asymmetrically kidney-shaped visual surfaces. Palpebral furrows adaxially curved; palpebral lobes biconvex-shaped. Palpebral lobes and eye socles are wide and swollen. The eyes interrupt the lateral border furrows anteriorly. Surface of the cephalon well ornamented with small to very small granules distributed all over the cephalon.

Description

Small trilobites with sagittal cephalic lengths from 3.8 to 6.5mm, the maximum cephalic width is slightly shorter than twice its length. The cephalic outline less the posterior margin is roughly semicircular with a smoothly forwardly curved anterior margin and smoothly rounded and parabolic genal angles. The posterior margin less the occipital ring is only very weakly forwardly curved. In front view the glabellar is convex; the genae are also convex but more weakly so than the glabella, the lateral borders are swollen. In side view the glabella slopes very weakly forward from its summit at the rear end of the frontal glabellar lobe. The anterior glabellar margin is thick and overhanging. The anterior border cannot be seen. To the rear of its summit the glabella immediately drops down into the preoccipital ring which is slightly lower than both the glabella and the occipital ring. The genae are tall. The posterior borders are swollen.

The glabella is inflated and expanded strongly forward. The glabellar angle is wide, ranging from 70^0 to 85^0. The postero-lateral glabellar margins are almost straight. The lateral glabellar corner is bluntly angled and the anterior glabellar margin is weakly curved forward. The S2 and S3 glabellar furrows are absent. The S1 preoccipital glabellar furrow is deep and narrow, continuous and curves forward medially. The lateral preoccipital pits are laterally elongated. The preoccipital ring is well defined and trilobed. The median preoccipital lobe is low, short, narrow and slightly planoconvex in outline while the lateral preoccipital lobes are lower than the median lobe, and laterally elongated with a rectangular or oval outline. The whole preoccipital ring is lower than the surrounding objects i.e. the frontal glabellar lobe, the occipital ring and the genae. The occipital furrow is deep and narrow, roughly straight medially. The lateral occipital pits are slightly shorter transversely than the lateral preoccipital pits. The occipital ring is wide, short and inflated, with roughly parallel sided margins both anteriorly and posteriorly.

The axial furrows are narrow and deep, and clearly separate the axial region from the genae and the borders. The genae are wide and quite inflated with the fixigenae and librigenae fused together. The anterolateral parts of the fixigenae are occupied by the small eyes. The librigenae are almost entirely restricted to the border. The border areas are separated from the genal region by the narrow and shallow border furrows. The border furrows continue round the genal angle; the lateral border furrows are interrupted by the eyes anteriorly. The posterior borders are more swollen than the lateral borders, and are narrow adaxially, widening abaxially and widest at the genal angle where they meet the lateral borders. The lateral borders which are also widest at the genal angle, narrow gradually forward. The genal angles are slightly swollen.

The facial sutures are obsolete but their traces remain on the cephalon. They are of proparian type, the traces appearing at their post-ocular branches and sometimes also present at their ocular branches. The post-ocular branches curve smoothly in an anterolateral direction from the rear end of the visual surfaces to the lateral cephalic margin just in front of the genal angles. The smooth inner margins of the visual surfaces indicate that the ocular branches of the facial sutures might be present there.

The cephalon lacks the ventral parts and anterior borders. The vincular furrow is seen only underneath the lateral cephalic margin; it is deep, narrow and continuous to the genal angle.

The eyes are small, situated on the anterolateral corners of the genae and protrude slightly from it in an anterolateral direction. The outlines of the eyes are roughly circular with their palpebral furrows adaxially curved. The palpebral furrows are narrow but quite deep, forming cusps anteriorly in between them and the axial furrows. The palpebral lobes are swollen, wide medially, narrowing both anteriorly and posteriorly. The boundary between the palpebral lobes and the visual surfaces are smoothly abaxially curved so that the palpebral lobes are biconvex-shaped medially. Anteriorly and posteriorly the palpebral lobes, although very narrow, are continuous until they meet the eye socles which bound the visual surfaces abaxially. The eye socles are swollen, crescentic in shape, wide medially, narrowing both anteriorly and posteriorly. The anterior lobes of the eye socles occupy the lateral border areas, interrupting the lateral border furrows. The bases of the eye socles fall into the detoured lateral border furrows anteriorly and form their own sulcus posteriorly where they rest on the genal fields. The inner margins of the eye socles are very roughly and irregularly outlined.

The visual surfaces are small, weakly sloping and asymmetrically kidney-shaped, wider anteriorly and narrower posteriorly. The inner margins of the visual surfaces are smoothly abaxially curved while their outer margins are roughly curved also in the abaxial direction. The visual surfaces are furnished with 16 to 23 small, circular and biconvex lenses (the diameter of the biggest lens reaches 0.30mm). These lenses are loosely packed and individually set in a hexagonal rim of sclera. All these lenses are arranged in 9 dorsoventral rows with a maximum 3 or 4 lenses in the longest rows.

The surface of the cephalon is heavily granulated. The small hemispherical granules (maximum diameter is 0.2mm) are distributed at random all over the cephalon. Generally granulation is heavier on the centre of the frontal glabellar lobe, the genae and the occipital ring. The other parts have lighter and slightly finer granules and on the lateral borders granulation is sparser and finer than on the other parts. A few granules can also be seen on the lateral preoccipital lobe. There is no mesial tubercle on the occipital ring.

Generally the granules are coarser in the central parts of the glabella and genae and finer peripherally.

Thorax: Some of the thoracic segments are preserved together with the cephalon; they reveal features similar to those of other phacopids.

No pygidia have been observed.

Comparison and discussion

Morphologically this subspecies is similar to those figured by R. & E. Richter (1926, pl.8, fig. 43) under Ph. wedekindi and by

Osmolska (1958, pl.1, figs. 2a,b) under *Ph. wedekindi wedekindi*.

Ph. wedekindi microps differs from *Ph. wedekindi occidentalis* n.ssp. in having a shorter eye length with an almost rounded eye outline, a smaller number of lenses; less strongly interrupted lateral border furrows; wider glabellar angle with straighter posterolateral glabellar margins and a more pronounced preoccipital ring. Furthermore, the granulation of *Ph. wedekindi occidentalis* is slightly coarser than that of *Ph. wedekindi microps*, and the mesial tubercle which is present in *Ph. wedekindi occidentalis* is absent in *Ph. wedekindi microps*.

Ph. wedekindi wedekindi R. & E. Richter and *Ph. wedekindi uralicus* Maksimova differ from *Ph. wedekindi microps* in having a larger eye (see table 2.2, p.28f), a narrower glabellar angle, strongly interrupted lateral border furrows and a weakly defined preoccipital ring.

Cryphops? *wocklumeriae* (R. & E. Richter) and *Cr*? *ensae* (R. & E. Richter) differ from *Ph. wedekindi microps* in having a smaller eye, crescentic-shaped palpebral lobes and uninterrupted lateral border furrows.

Strong differences between *Ph. wedekindi microps* and other subspecies of *Ph. wedekindi sensu lato* strongly support its subspecies status.

Remarks on the subspecific classification of *Ph. wedekindi sensu lato* R. & E. Richter

The description of *Ph. wedekindi* by R. & E. Richter in 1926, is seemingly too broad; it covers all forms between *Ph. granulatus* Münster and the genus *Cryphops*. In their description they outlined some characteristic features of this species in comparison to *Ph. granulatus* and to genus *Cryphops*, among others are statements translated as below.

"In respect to *granulatus*, *wedekindi* has :-

1. An adaxially curved palpebral furrow and a biconvex-shaped palpebral lobe.
2. An abaxially inclined palpebral lobe.
3. A shorter eye.
4. The extension of the eye onto the border (i.e. the interruption of the lateral border furrow) is greater than in *granulatus*. In an internal mould due to the shortness of the eye, the palpebral furrow is more significantly curved inward and the palpebral lobe is wider.

In respect to the *Ph.* (*Cr*?) *ensae* and *wocklumeriae*, *wedekindi* has the following marked distinctions :-

1. The characteristic of lateral border furrow (i.e. interrupted at the eye).
2. The extension of the eye onto the border.
3. The greater amount of lenses.
4. The steeply sloping visual surface.
5. The outward (abaxial) curve of the inner visual surface. "

These criteria have been used by later authors, namely Maksimova (1955), Osmolska (1958), Selwood (1960) and Chlupac (1966, 1977^{i}) in assigning their local collections of *Ph. wedekindi*. Osmolska (1958) and Selwood (1960) however mentioned that their local species has a smaller eye than those of R. & E. Richter.

Maksimova (1955) has assigned her specimens into a new subspecies i.e. *Ph. wedekindi uralicus* Maksimova, using the differences in the in the general shape of the glabella and the cephalon and the slope of the visual surface. The present author has some doubt as to the validity of this subspecies since the eye details of *Ph. wedekindi uralicus* are very similar to the holotype of the species and some other specimens of *Ph. wedekindi*, belonging to the R. & E. Richter collection. (see table 2.2, p.28f, and text-figure 2.2, p.28f). The importance of the number of dorsoventral files in subspecific classification of the phacopids has been discussed by many authors including Burton (1969), Burton and Eldredge (1974), Clarkson (1966) and Eldredge (1971). Eldredge (1971) also adds that some morphological variations might only represent a local variation of the subspecies.

Osmolska (1958), in order to distinguish her specimens from *Ph. wedekindi uralicus* has grouped all R. & E. Richter's collection into *Ph. wedekindi wedekindi* R. & E. Richter, in which she also includes her specimens into the same subspecies. However she remarked that her specimens have a smaller eye than those of R. & E. Richter.

Selwood (1960) and Chlupac (1966, 1977[i]), do not assign their specimens into any subspecies.

During the present research members of *Ph. wedekindi sensu lato* including those of the study area, the Launceston and Rhenish Mountains areas were studied, along with the figures and tabulated data published by Maksimova (1955), Osmolska (1958) and Chlupac (1966).

From this study *Ph. wedekindi sensu lato* can be divided into 3 groups i.e. *Ph. wedekindi wedekindi* + *Ph. wedekindi ?uralicus*,

→
Table 2.2
text-figure 2.3
" " 2.4

Table 2.2 The eye differences between the subspecies of Ph. wedekindi sensu lato

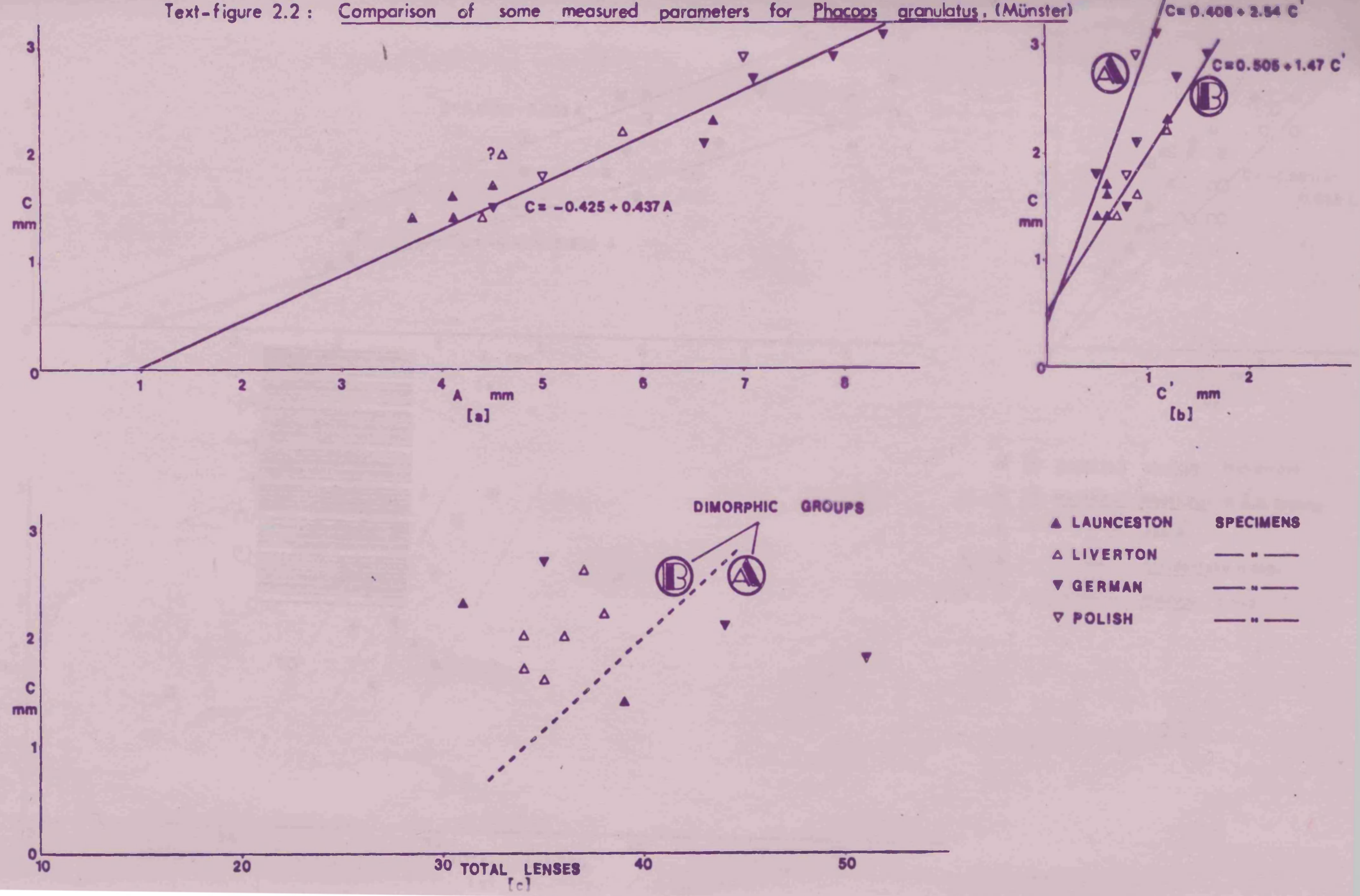
	Ph.w. uralicus	Ph.w. wedekindi	Ph.w.occidentalis	Ph.w. microps	Ph.w. ssp. A
Eye size	Medium to quite large	Medium to quite large	Medium	Small to medium	Medium
C/A	0.33-0.60	0.32-o.38	0.275-0.33	0.225-0.27	-
C/C'	-	1.40-2.14	1.2.-1.44	0.70- 1.10	-
Total lenses	30-46	?31-46	27-30	16-23	27-28
Total DV rows	13	13	9-10	9	11
Visual surfaces slope	very steep	steep	moderate to steep	moderate to steep	moderate to steep

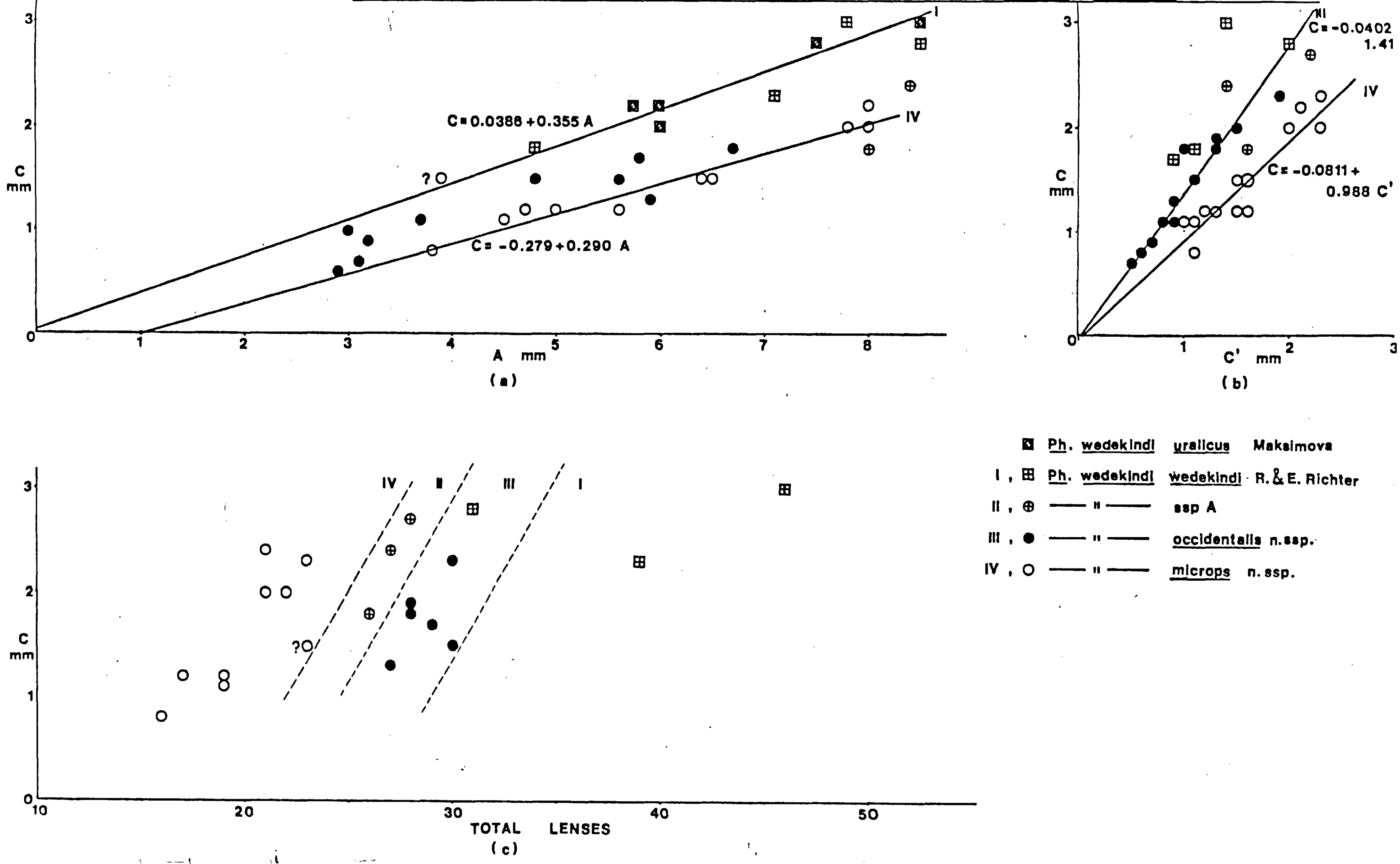
Note: Ph. wedekindi wedekindi (excluding specimen no. Rx 574e of R. & E. Richter and specimen no. I.G. 16911.6 of Osmolska). These two specimens were included in Ph. wedekindi microps together with the British specimens (from Launceston and Lounston).

DV ≡ dorsoventral, w.≡wedekindi

For other abbreviations see text-figure 1.3, p. 8f

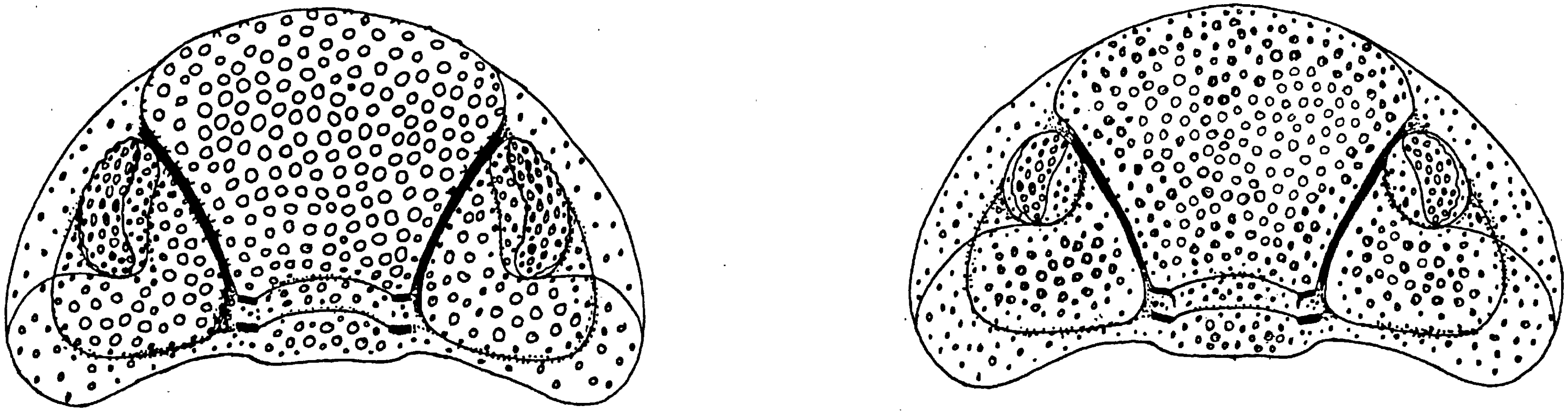
Text-figure 2.2 : Comparison of some measured parameters for *Phacops granulatus*. (Münster)





Text-figure 2.3 : Comparison of some measured parameters for all subspecies of *Phacops wedekindi*, R.& E. Richter

Text-figure 2.4 : Reconstruction of the sighted phacopid trilobites studied

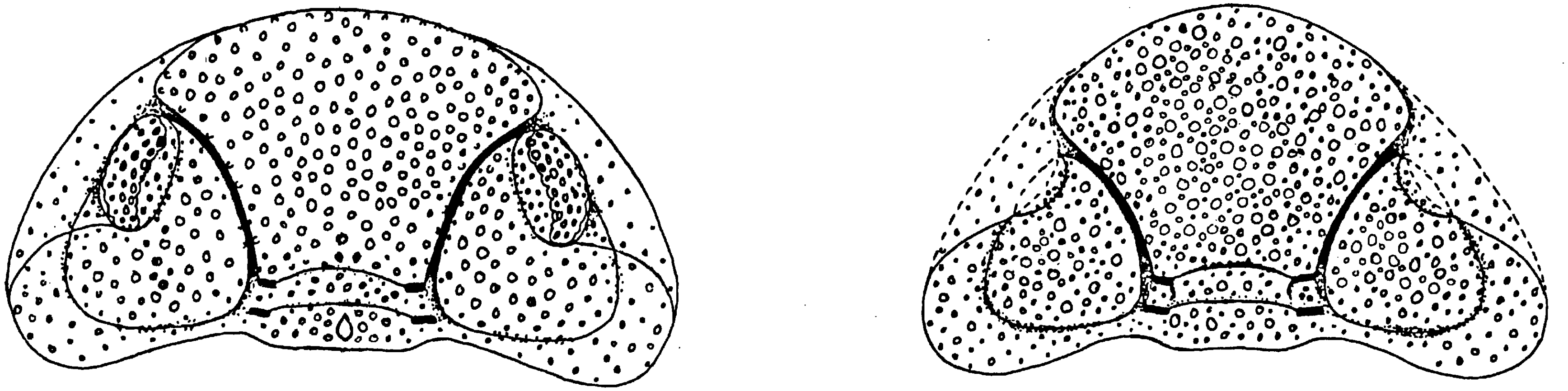


a. Phacops granulatus, (Münster)

(I.G.S. Zo 4529 X 8.62)

c. Phacops wedekindi microps ssp. nov

(PARATYPE II I.G.S. Zo 4559 X 7.57)



b. Phacops wedekindi occidentalis ssp. nov.

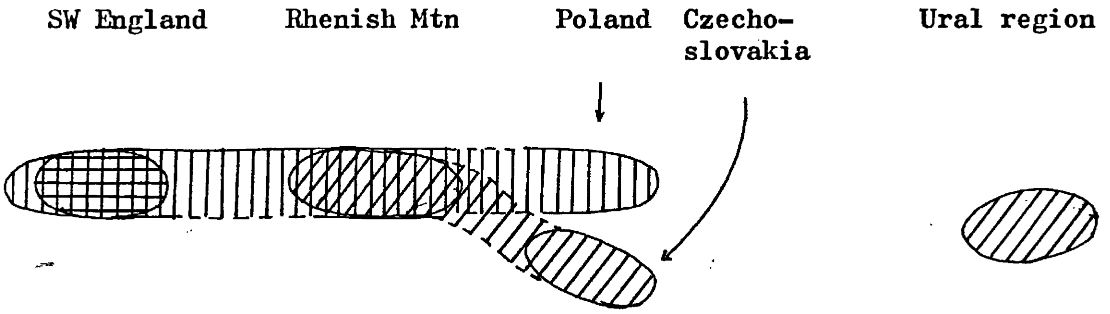
(HOLOTYPE I.G.S. Zo 4541 X 7.46)

d. Cryphops wocklumeriae lounstonensis ssp. nov

(PLASTOTYPE I.G.S. Zo 4589 X 12.5)

Ph. wedekindi occidentalis n.ssp. and *Ph. wedekindi microps* n.ssp. Their differences are mostly related to the construction of their eyes (see table 2.2 and text-figure 2.3, p.28f). For further comparisons between *Ph. wedekindi microps* and other groups, see p.26, while comparisons between *Ph. wedekindi occidentalis* and other groups can be seen on p.36. As in the other phacopid species, the grouping in *Ph. wedekindi sensu lato* as mentioned above can also be correlated geographically, which means that the subspeciation in this species is a geographical subspeciation (see table 3.4, for the distribution of the subspecies). The geographical relationships of the subspecies of *Ph. wedekindi sensu lato* can be briefly summarized as in the text-figure 2.5 below.

Text-figure 2.5 Geographic relationships between the subspecies of *Ph. wedekindi sensu lato*.



▥ *Ph. wedekindi microps* n.ssp.
▤ *Ph. wedekindi occidentalis* n.ssp.
▨ *Ph. wedekindi wedekindi* R. & E. Richter
+ ?*uralicus* Maksimova

→

Plate I

Plate II

EXPLANATION OF PLATE I

Figures 1-7. Phacops granulatus (Münster 1840)

1-4. Zo 4529 (LC); locality 1A (Lounston fossil band); 1-3 original carapace (Zo 4529a) showing plan, side and front views (x5, coated with ammonium chloride); 4 - latex cast of the external mould (Zo 4529b), front view shows the eye detail and the anterior border furrow (x5, coated with magnesium oxide).

5. Zo 4533 (LC); locality 1A (Lounston fossil band); internal mould (Zo 4533a), plan view (x5, coated with ammonium chloride).

6. AD 1896/7 (WC), locality 1D (Lounston fossil band), plasticine cast of the external mould (AD 1896), plan view shows granulations (x5, coated with ammonium chloride).

7. AD 1124 (WC); locality 3 (Ramshorn Down path), internal mould, plan view (x5, coated with magnesium oxide).

Figures 8-15. Phacops wedekindi occidentalis n.ssp.; locality 1A (Lounston fossil band), (LC).

8-9. Zo 4541, HOLOTYPE ; 8 - internal mould (Zo 4541a), plan view (x7, coated with ammonium chloride); 9 - latex cast of the external mould (Zo 4541b), plan view (x5, coated with ammonium chloride).

10-11. Zo 4542, PARATYPE; 10 - latex cast of the external mould (Zo 4542b), plan view (x5, coated with ammonium chloride), 11 - latex cast from the external mould (Zo 4542a), ventral view (x5, coated with magnesium oxide).

12. Zo 4543, internal mould, plan view (x5, coated with ammonium chloride).

13. Zo 4547, latex cast of the external mould (Zo 4547b), plan view (x9, coated with ammonium chloride).

14. HMA 21151, latex cast of the external mould (HMA 21151b), plan view, (x5, coated with ammonium chloride).

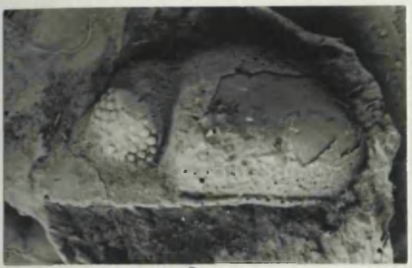
15. Zo 4555, juvenile, plan view shows the genal spine (x9 coated with ammonium chloride).

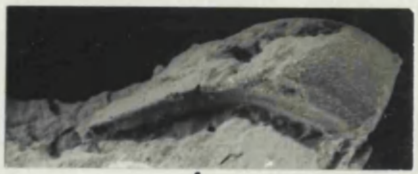
PLATE I


1

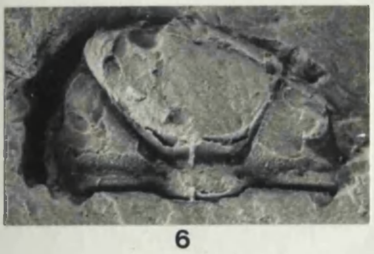

3


5


2


4

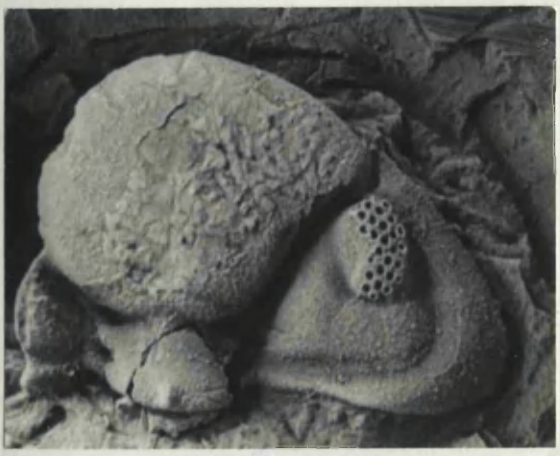

10


6


7


11

12



8

13


9


14


15


EXPLANATION OF PLATE II

1-2. *Phacops wedekindi wedekindi* R. & E. Richter 1926, HOLOTYPE (Rx 574c), from the Apricke locality of Iserlohn, W. Germany; plan and side view (x5, coated with magnesium oxide). This specimen is also figured in R. & E. Richter 1926, pl.8, fig.40. This specimen is of Richter's collection, lodged in Senckenberg Museum, Frankfurt.

3-7. *Phacops wedekindi microps* n.ssp.; 3-5, 7, from locality 1A (Lounston fossil band), 6 - from locality 1D (Lounston fossil band).

3. Zo 4559 (LC), latex cast of the external mould, plan view (x5, coated with ammonium chloride).

4. Zo 4558a (LC), actual carapace, plan view (x5, coated with magnesium oxide). Crushed specimen.

5. Zo 4574a (BC), internal mould, plan view (x5 coated with ammonium chloride).

6. AD 1891/2 (WC), internal mould, plan view (x5, coated with ammonium chloride).

7. Zo 4560a (LC), actual carapace, plan view (x5, coated with ammonium chloride).

8-9. *Phacops wedekindi* ssp. A.; locality 1A (Lounston fossil band)(LC)

8. Zo 4576a, internal mould, plan view (x5, coated with ammonium chloride).

9. Zo 4577a, internal mould, plan view (x5, coated with ammonium chloride).

10-11. *Phacops* (*Omegops*) Sp.B; - AD 2163(WC); locality 9 - internal mould, plan and side view (x5, coated with ammonium chloride).

12-14a. *Phacops* sp. indet. (pygidium)

12. Zo 4635 (LC); locality 1A (Lounston fossil band), plasticine cast of the external mould, plan view (x5, coated with ammonium chloride).

13. Zo 4636 (LC); locality 1A (Lounston fossil band), actual carapace, plan view (x5, coated with ammonium chloride).

14a. AD 1868 (WC); locality 1D (Lounston fossil band), actual carapace, plan view (x5, coated with ammonium chloride).

14b-15. *Cryphops*? *ensae* R. & E. Richter 1926 - locality 1D (Lounston fossil band) (WC).

14b. AD 1868, cephalon with part of carapace, plan view (x5, coated with ammonium chloride). Juvenile

15. AD 1859, cephalon with part of carapace, plan view (x5, coated with ammonium chloride).

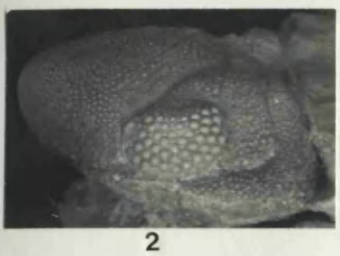
16. *Cryphops* sp. A - AD 1881/90 (WC); locality 1D (Lounston fossil band), internal mould with pygidium and part of thorax, plan view (x5, coated with ammonium chloride).

PLATE II


1


5


6


2


3

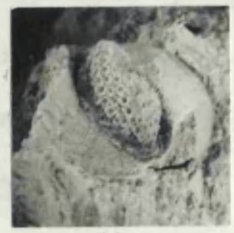

4


9


8


7

10


11


14a

14b

16


12

13


15

2.2.3 *Phacops wedekindi occidentalis* subsp. nov.

(Plate 1, figure 8-15, text-figure 2.4b, p.28f).

Deriv. nom.: From "occidens", a latin word for "western". *Phacops wedekindi occidentalis* n.ssp. represents the westernmost group of *Phacops wedekindi sensu lato*.

Holotype: Specimens Nos Zo4541a,b(part and counterpart) from the present author's collection have been chosen as a holotype, being the best preserved and the largest of the specimens.

Paratype: Specimens Nos. Zo4542a,b(parts, broken) from the present author's collection were chosen as a paratype, showing a better cephalic curvature than that of the holotype.

Localities: Localities 1A and 1D of the Lounston fossil band and locality 5 (see text-figure 1.2a & b, p.5f).

Horizons: The Rora Slate (Zone Vβ to VIβ).

- The Lounston fossil band is in the *sphaeroides* subzone (≡ Zone VI β of the Famennian) as indicated by the presence of the clymenids *Epiwocklumeria*.
- Locality 5 is in the *paradoxa* Zone (≡ Zone VI β of the Famennian) as indicated by the presence of the clymenid *Parawocklumeria*.

Materials: 16 specimens from locality 1A, 1 specimen from locality 1D and 2 specimens from locality 5.

Locality 1A - specimens Nos. Zo4531, 4541-4555 (LC), Zo4557, 4624-4625 (BC) and HMA21151 (LC).

Locality 1D - specimen No. AD1891/2 (1 specimen) (WC).

Locality 5 - specimens Nos. AD1980 (2 specimens)(WC).

Preservation: In general the condition of preservation is not very good.

Diagnosis.

Cephalic outline longer than semicircular; glabella not strongly inflated, but strongly expanded forward with the posterolateral glabellar margin bent strongly outward near the lateral glabellar corner. Lateral glabellar corners form a beak-like projection. The anterior glabellar margin is overhanging. S2 and S3 glabellar furrows are absent. S1 preoccipital glabellar furrow shallow but continuous and curved forward medially. Preoccipital ring not well defined; low and unobtrusive; its lateral lobes poorly distinguished. Occipital ring has a mesial tubercle. Axial furrows wide but shallow. Genae less inflated than the glabella. Facial suture obsolete. Anterior doublure short. Vincular furrow wide and deep medially, narrowing laterally, continuous to the genal angle. Eyes of medium size compared to the genal field, oval shaped with asymmetrically kidney shaped visual surfaces. Palpebral furrows, shallow and adaxially curved; palpebral lobes swollen. Eye socles narrow and occupying the border region anteriorly. Surface of the cephalon well granulated.

Description

Small trilobites with a sagittal cephalic length from 3.1mm to 8.4mm and a maximum cephalic width nearly twice the length. The cephalic outline less the posterior margin is slightly longer than semicircular and smoothly curved forward anteriorly. The genal angles are rounded and parabolic, and project strongly rearward so that the posterior margin less the occipital ring forms a smooth anterior curve which sometimes becomes significantly stronger due to distortion. In front view the glabella is weakly convex, and genae being even less convex. The lateral borders are swollen, being separated from the genae by the well marked border furrows. In side view the profile of the cephalon is low with the glabellar summit situated slightly in front of the preoccipital ring. From the summit forward, the glabella slopes very weakly and steadily toward a thin and overhanging anterior glabellar margin. From the summit rearward, the glabella falls down sharply to the low and unobtrusive preoccipital ring. The occipital ring at the rear end of the cephalon is obtrusive.

The glabella is weakly inflated, narrow posteriorly and expands strongly anteriorly. The glabellar angle ranges from 58° to 77° posteriorly but expands anteriorly to about 90° to 100° when it reaches the lateral glabellar corner. The posterolateral glabellar margins are strongly bent outward anteriorly near the lateral glabellar corners. The lateral glabellar corner forms a beak-like projection. The anterior glabellar margin is smooth and curves weakly forward. The S2 and S3 glabellar furrows are absent. The S1 preoccipital glabellar furrow is narrow and shallow but continuous and curves forward medially. The lateral preoccipital pits are transversely elongated but sometimes they are almost circular in outline. The preoccipital ring is short, narrow, low, unobtrusive and poorly defined. The lateral preoccipital lobes are poorly developed, almost indistinguishable from the median lobe. The occipital furrow like the S1 preoccipital glabellar furrow, is shallow and narrow but continuous and curves forward medially, but the curve of the former is slightly weaker than that of the latter. The lateral occipital pits are transversely elongated, being slightly longer transversely than that of the lateral preoccipital pits. The occipital ring is short, narrow, quite obtrusive and biconvex in shape. The mesial tubercle is slightly elongated sagittally and forms a spine like projection.

The axial furrows are quite wide but shallow. The genae are quite wide, low and weakly inflated. The anterolateral corner of the genae being occupied by the eyes. The facial sutures are obsolete but their traces remain along the lines of separation of the fixigenae from the librigenae. Only the postocular branches of the facial sutures are found, they appear at the rear end of the visual surfaces, curving smoothly in an anterolateral direction until they meet the lateral cephalic margins shortly in front of the genal angles. Most of the librigenae are in the border region. The border region is separated from the genal field by narrow and shallow border furrows. The lateral border furrows are interrupted at the eyes, following the baseline of the eyes. The posterior borders are narrow and swollen, widening from the occipital ring abaxially to the genal angles where they are widest and here meet the lateral borders. The lateral borders from their widest at the genal angles narrowing gradually forward, interrupted at the eyes and the lateral glabellar corners. The lateral borders are swollen posteriorly, gradually flattening forward. The anterior border is wide and flattened laterally, narrow and swollen medially. The anterior border furrow is narrow, shallow and continuous medially. The anterior doublure is narrow and crescentic in outline with both its posterior and anterior margins forwardly curved. The vincular furrow is wide and deep medially, narrowing but remaining of approximately the same depth laterally. It is continuous, following the lateral cephalic margins toward the genal posterior extremities. The hypostomal suture curves smoothly forward. The post-vincular doublure is wide medially and narrow laterally.

The eyes are of medium size and their general outlines are slightly oval-shaped. The palpebral furrows are narrow, shallow and adaxially curved, meeting the axial furrows at a very narrow angle anteriorly. The palpebral lobes are wide medially, narrowing both posteriorly and anteriorly, meeting the eye socles in front and at the rear end of the visual surfaces. The palpebral lobes are swollen and bounded adaxially by the palpebral furrows, while their outer margins are bounded by the irregular abaxial curves between them and the top scleral rims of the visual surfaces. The eye socles are crescentic in shape, curving abaxially, very narrow and weakly swollen, narrowing posteriorly and anteriorly until sometimes the visual surfaces rest entirely on the border. The bases of the eyes almost always interrupt the lateral border furrows where at least the anterior half of the eye socles or the visual surfaces occupy the lateral border region. The visual surfaces slope weakly and are asymmetrically kidney-shaped. They are long, narrow and bounded by an irregular outline both at the inner and outer margins. The visual surfaces carry 27 to 30 small (maximum diameter 0.25mm), rounded (in outline) and biconvex lenses. These lenses are set in hexagonal rims of sclera and arranged in 9 to 10 dorsoventral rows. The maximum number of lenses per row is 4. The front rows are usually longer than the rear one. The lenses are smaller in the bottom horizontal rows, gradually increasing in size to the top. The topmost lenses of a few middle dorsoventral rows are smaller than the other lenses in the same visual surface.

The surface of the cephalon is very well granulated (on the carapace and the external mould); the internal mould is usually smooth. The ornamentation is made of fine hemispherical granules (diameter up to 0.20mm) distributed randomly and densely on the centre of the glabella and genae. The other parts are only ornamented by few, and sparsely distributed smaller granules. A single mesial tubercle which looks like a spine projection can be seen on the occipital ring.

Ontogeny (plate 1, figure 15)

Some juvenile phacopids, probably late meraspids, were found, bearing spines on their genal angles and bearing a mesial tubercle on the occipital ring. Since there are no other mesial tubercle-bearing phacopids in the study area the present author presumes that these juveniles belong to this subspecies, i.e. Ph. wedekindi occidentalis n.ssp. These juveniles when compared to their adults, have a more convex glabella and genae, a wider glabellar angle, strongly marked furrows (including the axial furrows, border furrows, occipital furrow and S1 preoccipital glabellar furrow) and a functional facial suture. Compared to the juveniles of Cryphops? wocklumeriae lounstonensis n.ssp., the juveniles of Ph. wedekindi occidentalis have a more convex glabella and genae, a regular granulation and mesial tubercles on their occipital rings.

Early holaspids which show very similar features to those of the juveniles were also found (see plate 1, figure 13). These holaspids differ from the meraspids by having no genal spines and having a non-functional facial suture. Differing from larger adults, these young holaspids have a smaller number of lenses though the number of dorsoventral rows is similar; a more steeply sloping visual surface, a more inflated glabella and genae and a wider glabellar angle.

Comparison and discussion

Phacops wedekindi occidentalis is similar to other members of *Phacops wedekindi sensu lato* in having a small (compared to the other species of *Phacops*) eye with adaxially curved palpebral furrow and with parts of the eye socle occupying the border region. It is also similar to the other members of *Ph. wedekindi sensu lato* in having a strongly granulated carapace and a rather weakly developed preoccipital ring.

Ph. wedekindi occidentalis differs from *Ph. wedekindi wedekindi* R. & E. Richter (1926) and *Ph. wedekindi uralicus* Maksimova (1955) in having smaller eyes (smaller in size, number of lenses and dorso-ventral rows), with less steeply sloping visual surfaces (see table 2.2, p.28f and text-fig. 2.3, p.28f). The new subspecies also, in comparison to *Ph. wedekindi wedekindi* and *Ph. wedekindi uralicus*, has a stronger curve on its posterolateral glabellar margins which gives the lateral glabellar corners beak-like projections. Furthermore it has wider axial furrows and narrower occipital and preoccipital rings. The new subspecies also differ from other subspecies of *Ph. wedekindi sensu lato* in having a mesial tubercle on its occipital ring which the others do not possess.

The differences between *Ph. wedekindi microps* n.ssp. and *Ph. wedekindi occidentalis* n.ssp. were discussed in p. 26 (see also table 2.4, p.28f and text-figure 2.3, p.28f and 2.4, p. 28f).

Phacops granulatus which is also found in the same location differs from *Ph. wedekindi occidentalis* mainly by having a bigger eye (bigger in size, number of lenses and number of dorsoventral rows) with abaxially curved palpebral furrows, with the eye entirely restricted to the genal field. *Ph. granulatus* also differs from *Ph. wedekindi occidentalis* in having a straighter posterolateral glabellar margin, a wider and slightly more pronounced preoccipital ring and in having no mesial tubercle. (See text-figure 2.4, p.28f).

These minor but sharply defined differences, summed up in the discussion above and in p. 26 , are sufficient to warrant a subspecific status for this new form.

2.2.4 *Ph. wedekindi* ssp. A

(Plate 2, figures 8-9).

Locality: Locality 1A of the Lounston fossil band (see text-figure 1.2b, p.5f).

Horizon: The Rora Slate - *sphaeroides* subzone (≡ Zone VIβ of the Famennian) indicated by the presence of the clymenid *Epiwocklumeria*.

Materials: 3 specimens; nos. Zo 4576-4577, ?4578 (LC) - all are internal moulds.

Description

Small trilobites with sagittal cephalic lengths from 8.0mm to 8.4mm. The glabella is weakly inflated with the posterolateral glabellar margins curving outward slightly near the lateral glabellar corners. The lateral glabellar corners form cusps. The preoccipital ring is low and weakly defined. The lateral preoccipital and occipital pits are circular in outline. The axial furrows are narrow and deep anteriorly, shallow and obscure posteriorly. The genae are weakly inflated. The facial sutures are obsolete, traces of their postocular branches distinguish the librigenae from the fixigenae posteriorly. The border furrows are narrow and shallow. The posterior borders are narrow and swollen while the lateral borders are wider and less swollen compared to the former. The eyes are medium sized and slightly oval in shape. The palpebral furrows are narrow, shallow and curve adaxially anteriorly and are straighter posteriorly. The palpebral lobes are swollen, wide medially and narrowing anteriorly and posteriorly. The eye socles are wide posteriorly, narrowing forward and interrupt the lateral border furrows anteriorly. The visual surfaces are long but narrow, weakly sloping and asymmetrically kidney-shaped with irregular inner and outer margins. The visual surface carries 27-28 small (diameter up to 0.3mm), circular (in outline) and biconvex lenses. The lenses are set in hexagonal rims of sclera and arranged in 11 dorsoventral rows. The maximum lenses per row are 3. The front rows are longer than the back ones. The granulation of the cephalon is poorly preserved.

Comparison and discussion.

Phacops wedekindi ssp. A resembles the other members of *Phacops wedekindi sensu lato* in having adaxially curved palpebral furrows, interrupted lateral border furrows (at the eye), a weakly defined preoccipital ring and shallow axial furrows, palpebral furrows and border furrows.

Phacops wedekindi ssp. A resembles *Ph. wedekindi occidentalis* in having a very similar eye outline and similar ranges of eye size and total lens number, but the former differs from the latter in having narrower visual surfaces, wider eye socles, narrower axial furrows, a less strongly curving posterolateral glabellar margin and no mesial tubercle. For a given cephalic length, *Ph. wedekindi occidentalis* has a bigger number of lenses than does *Ph. wedekindi* ssp. A, but the former has 9 to 10 dorsoventral rows while the latter, i.e. *Ph. wedekindi* ssp. A, has 11 dorsoventral rows.

Ph. wedekindi microps and *Ph. wedekindi* ssp. A resemble each other in having narrow visual surfaces and wider eye socles, but the former differs from the latter in having a small eye size, a smaller total lens number and a smaller number of dorsoventral rows, a rounded eye outline and more pronounced axial furrows, border furrows and preoccipital ring. In comparison to *Ph. wedekindi wedekindi* and *Ph. wedekindi uralicus*, *Ph. wedekindi* ssp. A has a markedly smaller eye size, a smaller total lens number, and fewer dorsoventral rows of lenses.

The general features of the eye and preoccipital ring suggest that *Ph. wedekindi* ssp. A belongs to *Ph. wedekindi sensu lato*, while details of the eye, especially the orientation of lenses, distinguishes this subspecies from the other members of the species. However a bigger collection is needed before this subspecies can be referred either to one of the above subspecies or to a subspecies of its own.

2.2.5 *Phacops* sp. indet. (pygidium)

(Plate 2, figures 12-13).

Localities: Localities 1A, 1B and 1D of the Lounston fossil band (see text-figure 1.2b, p.5f), 3 and 5 (see text-figure

1.2a, p.5f).

Horizons: The Rora Slate (Zone Vβ to VIβ).

- Lounston fossil band - *sphaeroides* subzone (≡ Zone VIβ of the Famennian) indicated by the presence of the clymenid *Epiwocklumeria* sp.
- Locality 5 - *paradoxa* Zone (≡ Zone VIβ of the Famennian) indicated by the presence of the clymenid *Parawocklumeria* sp.
- The specific age of locality 3 is uncertain.

Materials: locality 1A - Zo 4635-4640(LC) and Zo 4641 (BC); locality 1D - AD 1868(WC); locality 3 - AD 1122 (WC); locality 5 - AD 1983(WC).

Remarks

These pygidial remains cannot be referred to any particular species of *Phacops* because of the absence of the other parts of the exoskeleton and because of the overall similarity of many of the pygidia in the genus. The pygidium is short with a sagittal length less than half the maximum width. The posterior margin is weakly curved. The axis tapers backward with the maximum width only slightly less than the sagittal pygidial length. It has 4 rings, and the terminal piece has a sagittal length almost equal to its width. The postaxial region is very narrow. The axial furrows are shallow and narrow, continuous posteriorly as a shallow depression. The pleural region has 3 pairs of pleural furrows indicating 3 pairs of ribs. The interpleural furrows as well as the border furrows are absent. The border area is small, indicated by a smooth area where the pleural furrows stop short laterally. The surface of the pygidium is well granulated. Fine hemispherical granules (diameter about 0.1mm) distributed on the higher relief of the pygidium, that is, on the rings, ribs, terminal pieces and the border region. The granules on the border are finer than that on the other parts.

Compared to the pygidia of Cryphops, these pygidia have a longer sagittal length, a more strongly curving posterior margin, longer terminal pieces, more rings and ribs and more ornament.

Compared to the pygidia of Phacops (Omegops) Struve (1976), these pygidia have a shorter sagittal length, less strongly curving posterior margin and less rings and ribs.

2. 3 Subgenus: Phacops (Omegops) Struve 1976

2.3.1 Phacops (Omegops) Sp. B.

(Plate 2, figs 10-11).

Locality: Locality 9 (see text-figure 1.2a, p.5f).

Horizons: The Rora Slate - Wocklumeria Stufe (≡ Zone VI of the Famennian) indicated by the presence of subgenus Phacops (Omegops).

Materials: 2 specimens Nos. AD 2163/4, 2165/6 (WC).

Remarks

One of the specimens (AD 2163/4) shows a well preserved right eye. The eye of this specimen shows a contrast between this species and Phacops (Omegops) of Struve. The eye of this species has 64 lenses which is within the range of Phacops (Omegops), but these lenses are arranged in 18 dorsoventral rows instead of 15 or 16 in other species of Ph. (Omegops). The maximum number of lenses per row is 5. In other respects the eyes of this species are similar to other species of Ph. (Omegops), very strongly curved abaxially with a very steeply sloped visual surface. The postocular genal fields are narrow and swollen as in other species of Ph. (Omegops). This species also resembles other species of Ph. (Omegops) in having a narrow glabellar angle (55^{0}) and a degenerate preoccipital ring. Phacops (Omegops) sp. B lacks granulation.

Thus the features shown by this species, excluding the orientation of the eye lenses and the granulation, strongly suggest that it belongs to the subgenus Phacops (Omegops). However the number of dorsoventral rows shown by the examples from the study area necessitate some revision of the subgenus, a revision which must wait for the assembly of a larger and more representative collection.

2.4 Genus Cryphops (R. & E. Richter, 1926.)

2.4.1. Cryphops? wocklumeriae lounstonensis subsp.nov.

(Plate 3, figures 3-8, text-figure 2.4, p.28f).

Deriv. nom.:	From "Lounston" - the name of the farm where the subspecies is found.
Holotype:	Specimen No. Zo 4579b was chosen to be the "holotype" of the subspecies on the basis that it is better preserved than the others and it is one of the largest and earliest specimens found (collected by Burton in 1968).
Plastotype:	Since the holotype consists of only the external mould, a "plastotype" (Zo 4579a) was produced by a latex cast.
Paratype:	Zo 4583 - Shows an actual carapace which is well granulated.
Locality:	Locality 1A of the Lounston fossil band (see text-fig. 1.2b, p. 5f).

Horizon: The Rora Slate - *sphaeroides* subzone (≡ Zone VIβ of the Famennian) diagnosed by the presence of the clymenid *Epiwocklumeria*.

Materials: 17 specimens.

Zo 4579-4581, 4626(BC), Zo 4583, 4585-4587, 4590-4592, 4594-4595, 4597-4590, 4600 (LC) and HMA 21153 (LC).

Preservation: Condition of preservation generally fairly good.

Diagnosis

Cephalic outline slightly longer than semicircular. Genal angle smoothly rounded and parabolic. Glabella inflated, expanding strongly forward with a gently curved posterolateral margin. The glabellar angle is wide. S3 glabellar furrow absent; S2 glabellar furrow very narrow and shallow; S1 preoccipital glabellar furrow shallow and narrow, continuous and curving forward medially. Lateral preoccipital and occipital pits transversely elongated. Lateral preoccipital lobes well developed. Occipital furrow weakly curving forward medially. Occipital ring obtrusive, no mesial tubercle. Axial furrows wide and deep. Genae inflated. Border furrows narrow and deep while border area narrow and swollen. Palpebral lobes are small, crescentic in shape and curving adaxially. Visual surface together with the rest of the librigenae absent, detached during moulting. Facial suture functional. Surface of cephalon heavily granulated with two different granular sizes occurring together.

Description

Small trilobites with sagittal cephalic lengths ranging from 2.3mm to 4.5mm, those specimens with sagittal cephalic lengths of 2.7mm or less being considered as juveniles (see p. 46).

In the adult the cephalic outline less the posterior margin is only slightly longer than semicircular but due to compression it sometimes becomes shorter than semicircular. The anterior cephalic margin is smoothly curved anteriorly, interrupted laterally along the suture line (note: all the adult specimens are moulted), continuous again posteriorly near the genal angles. The genal angles are smoothly rounded and parabolic. The posterior cephalic margin is weakly curved forward or nearly straight on the compressed specimens. In front view the glabella is convex. The genae are also convex with their lateral borders separated from them by the distinct border furrows. In side view the glabella is tallest at the rear end of the frontal glabellar lobe, sloping gently forward to the anterior margin. The anterior margin is thin, curves forward slightly, and is possibly overhanging in life position, but in the moulds (as in all the cases of the Lounston species) the anterior border is missing. Toward the rear end of its summit the glabella drops suddenly to the preoccipital furrow. The preoccipital ring is only a little lower than the glabella and the occipital ring.

The glabella is inflated and expands strongly forward. The glabellar angle ranges from 70° to 85°. The posterolateral glabellar margins bend outward anteriorly. The lateral glabellar corners are smoothly rounded. The anterior glabellar margin is strongly curved forward. The S3 glabellar furrows are absent. The S2 glabellar furrows are very narrow and shallow, short, converging forward but discontinuous medially. In the very well granulated specimen these furrows are marked by a line devoid of granules. The S1 preoccipital glabellar furrow is shallow and narrow, continuous and curves forward medially. The lateral preoccipital pits are wide and deep and transversely elongated. The preoccipital ring is well defined and divided into 3 lobes. The median lobe is short and narrow, almost planoconvex in outline separated by a shallow depression from the lateral preoccipital lobes which are rounded or square in outline. All the lobes are swollen with the median lobe being stronger than the lateral ones. The occipital furrow is shallow and narrow, continuous and is usually very weakly curved forward medially, but is sometimes straight medially. The lateral occipital pits are shorter transversely compared to the lateral preoccipital pits. The occipital ring is narrow, short and obtrusive.

The axial furrows are narrow and deep anteriorly, shallower and wider posteriorly beside the preoccipital and occipital rings. The genae are inflated with a small eye on their anterolateral corners. The librigenae are missing due to moulting. The facial suture is functional. The postocular branches of the facial suture are smoothly curved in an anterolateral direction from the rear end of the eyes to the lateral cephalic margins in front of the genal angles. The ocular branches of the facial suture are broken, presumably during fossilization. The preocular branches of the facial suture are also broken posteriorly but anteriorly they are well preserved. The facial suture runs along the base of the anterior glabellar margin so that the anterior border and the ventral parts are missing in the moulted specimens. The eye size was measured only by the length of the palpebral lobe though in most specimens this is broken. The palpebral furrows are narrow, quite deep and curve strongly adaxially. The palpebral lobes are swollen and have a crescentic shape, curving adaxially.

The surface of the cephalon is very well ornamented. There are two sizes of granules, both being hemispherical in shape, distributed all over the cephalon. The larger granules (diameter between 0.10 to 0.20mm) are distributed at random, at a distance from each other, concentrated on, the central parts of the glabella and genae, rarer on the peripheral parts of the glabella and genae, the occipital and preoccipital rings the palpebral lobes and the border regions. The smaller granules (diameter less than 0.10mm) are situated in between the larger granules. In contrast with the larger granules the smaller granules are concentrated on the places where the former are rare, that is on the border region, the palpebral lobe, the occipital and preoccipital rings (including the lateral preoccipital lobes which are devoid of bigger granules) and on the peripheral parts of the glabella and the genae. There is no mesial tubercle on the occipital ring.

Ontogeny

The specimens having a cephalic length of less than 2.7mm show distinct differences when compared with the larger forms of the species. These small specimens are of late meraspid age diagnosed by the presence of the genal spines. The juveniles when compared to the adults have a more convex glabella, wider glabellar angle, less distinct S2 glabellar furrow, S1 preoccipital glabellar furrow and occipital furrow. Furthermore the preoccipital ring of the juvenile is not as well defined as it is in the adult, and the lateral preoccipital lobes in the adult are better developed than that of the juvenile. The posterior cephalic margin of the juvenile curves more strongly than that of the adult.

The ornamentation on the adult and the juvenile is similar.

Comparison and discussion

Cr? wocklumeriae lounstonensis n.ssp. differs from other species of *Cryphops* mainly by the presence of the functional facial sutures, although for the same reason the eye of this subspecies is missing and cannot be compared with other species of *Cryphops*.

Cr? *wocklumeriae lounstonensis* resembles other members of the species in having a similar granulation pattern, similar shapes of glabella, genae and palpebral lobes. Differences from *Cr*? *wocklumeriae wocklumeriae* (R. & E. Richter 1926) include a more strongly marked S1 preoccipital glabellar furrow medially, more distinct lateral preoccipital lobes and a functional facial suture.

Cr? *ensae* (R. & E. Richter 1926) resembles this species in having quite well developed lateral preoccipital lobes and similar sized palpebral lobes. In contrast to the new subspecies, *Cr*? *ensae* has a narrower glabella and genae, a less strongly marked S1 preoccipital glabellar furrow medially, a non-functional facial suture and a mesial tubercle on its occipital ring.

The new subspecies can be distinguished from other species and subspecies of *Cryphops* (apart from the two above) by its functional facial suture, well developed lateral preoccipital lobes, well marked S1 preoccipital glabellar furrow and well granulated carapace with large and small granules occurring together in the same place.

The above comparison provides strong differences between *Cr*? *wocklumeriae lounstonensis* n.ssp. and the other established species and subspecies of *Cryphops*, thus supporting its new subspecific status.

Note on *Cryphops*? *schlosseri* (R. & E. Richter 1955)

Cr? *schlosseri*, the other form of *Cryphops* which has a functional facial suture, is in strong contrast to *Cr*? *wocklumeriae lounstonensis* and other species and subspecies of *Cryphops* in having triangular palpebral lobes with angular palpebral furrows, interrupted lateral border furrows at the eyes, a straight S1 preoccipital glabellar furrow and a smooth cephalic surface. These features in which *Cr*? *schlosseri* differs from other species of *Cryphops*, in fact belong to the genus *Dienstina* (R. & E. Richter 1931). Compared to other species of *Dienstina*, *Cr*? *schlosseri* has well developed lateral preoccipital lobes, a slightly wider glabellar angle and a functional facial suture. These very small differences suggest that *Cr*? *schlosseri* is better placed in the genus *Dienstina* instead of *Cryphops*. So *Dienstina schlosseri* (R. & E. Richter) is the form of this genus with a functional facial suture.

2.4.2 *Cryphops? ensae* (R. & E. Richter 1926)
(plate 2, figures 14b-15)

1926 *Phacops* (*Cryphops*?) *ensae* R. & E. Richter, p.164-167 pl. 9, figs. 61-66.

1954 *Phacops* (*Cryphops*?) *ensae* R. & E. Richter; Pfeiffer, p.40-41, pl.2, fig. 4.

1960 *Phacops* (*Cryphops*?) *ensae* R. & E. Richter; Selwood; p.177.

1975 *Cryphops*? *ensae* R. & E. Richter; G. & H. Hahn, p.25, pl.2, fig. 18.

Locality: Locality 1D of the Lounston fossil band (see text-fig. 1.2b, p.6).

Horizons: The Rora Slate - *sphaeroides* subzone (≡ Zone VI β of the Famennian) diagnosed by the presence of the clymenid *Epiwocklumeria*.

Materials: AD 1859 and AD 1868 (WC).

→
Plate III

EXPLANATION OF PLATE III

1-2. *Cryphops? wocklumeriae wocklumeriae* (R. & E. Richter 1926) Richter's collection in the Senckenberg Museum, Frankfurt.

1. HOLOTYPE (Rx 564c) from the Hönne-Tal locality of Balve, W. Germany; original carapace, plan view (x5, coated with magnesium oxide); this specimen is also figured by R. & E. Richter (1926), pl. 9, fig.65.

2. Rx 564c from the Hönne-Tal locality of Balve, W. Germany, original carapace, plan view (x5, coated with magnesium oxide).

3-8. *Cryphops? wocklumeriae lounstonensis* n.ssp. - locality 1A (Lounston fossil band).

3. Zo 4579a (BC), PLASTOTYPE, plan view (x6, coated with magnesium oxide).

4. Zo 4583a (LC), PARATYPE, plan view (x5, coated with magnesium oxide).

5. Zo 4581a (BC), juvenile, plan view shows shifted librigena, genal spine, part of thorax and transitory pygidium in "salterian moult" type of ecdysis, (x6, coated with ammonium chloride).

6. Zo 4590 (LC), cephalon with part of carapace and internal mould, plan view shows a suture line (postocular branch), (x5, coated with ammonium chloride).

7. Zo 4585a (LC), original carapace, plan view (x6, coated with ammonium chloride).

8. Zo 4594 (LC), cephalon with part of carapace and internal mould, plan view shows attached librigena and ?genal spine (x6, coated with ammonium chloride).

9-12. *Dianops griffithides griffithides* (R. & E. Richter 1919)(LC).

9-11. from locality 1C (Lounston fossil band); 12, from locality 1A (Lounston fossil band).

9. Zo 4664, latex cast of the external mould (Zo 4664a), plan view shows fine granules (x5, coated with ammonium chloride).

10. Zo 4663, cephalon and thorax with part of carapace and internal mould, plan view (x5, coated with ammonium chloride).

11. Zo 4668, internal mould of cephalon and thorax in "salterian moult" mode of ecdysis, plan view (x3, coated with magnesium oxide).

12. Zo 4614a, internal mould of the cephalon, plan view (x3, coated with ammonium chloride).

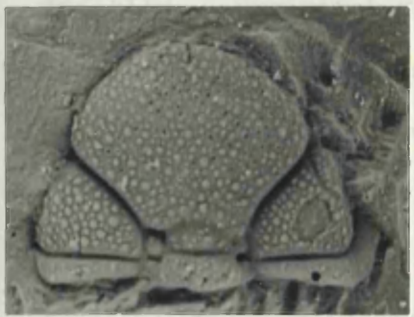
13. *Dianops* sp. A; AD1862 (WC), locality 1D (Lounston fossil band), internal mould, plan view (x5, coated with ammonium chloride).

PLATE III

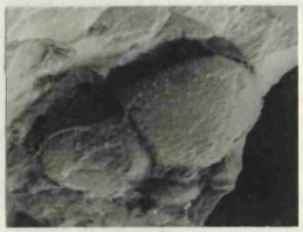

1


2


4


3


5


6


7


8


11


13


12


10

Diagnosis

Cephalic length longer than semicircular, smoothly curved anteriorly and almost straight posteriorly. Genal angle smoothly rounded and parabolic. Glabella strongly expanding forward, convex and inflated. Preoccipital ring poorly developed, low and unobtrusive. S1 preoccipital glabellar furrow shallow, narrow and curving forward medially. Occipital ring obtrusive. Axial furrows wide and deep. Genae inflated. Posterior borders narrow and swollen. Lateral borders wider than posterior border and less swollen. Facial sutures cannot be traced in the adult but well developed in the juvenile. Eye small and oval shaped. Palpebral furrow narrow and shallow, palpebral lobe weakly swollen. Eye socle narrow. Visual surface oval shaped and bearing 9 lenses. Surface of the cephalon lacks granulation.

Description

A small trilobite with a sagittal cephalic length 4.3mm (the juvenile has a sagittal cephalic length 2.8mm). The cephalic outline is longer than semicircular. The anterior cephalic margin is smoothly curved forward while the posterior cephalic margin is straight medially and curves anterolaterally at its distal ends. The genal angles are smoothly rounded and parabolic. In front view the glabella and genae are convex, the former is more strongly convex; the lateral borders are slightly swollen. In side view the glabella forming a summit at the rear end of the frontal glabellar lobe, slopes steadily forward and drops sharply backward to the preoccipital glabellar furrow. The anterior glabellar margin is thin and overhanging in side view. The preoccipital ring is slightly lower than the glabella and the occipital ring.

The glabella is inflated and expands quite strongly forward.

The glabellar angle is narrow (60^{o} in the adult) at the entrant angle and as the axial furrows move forward this angle widens. The posterolateral glabellar margins bend outward toward the lateral glabellar corners which are slightly angular. The anterior glabellar margin curves strongly forward. The S2 and S3 glabellar furrows are absent. The S1 preoccipital glabellar furrow is shallow and narrow, continuous, and curves forward medially. The lateral preoccipital and occipital pits are wide, deep and transversely elongated. The preoccipital ring is poorly developed. It is short, narrow and low with the lateral lobes almost inseparable from the median lobe. The occipital furrow is shallower, narrower and curves medially more weakly than the S1 preoccipital glabellar furrow. The occipital ring is short, narrow and quite obtrusive.

The axial furrows are wide and deep. The genae are inflated but weaker than both the frontal glabellar lobe and the occipital ring. The eyes are small and situated on the anterolateral corner of the genae. The facial sutures cannot be traced so that the librigenae are inseparable from the fixigenae. The border furrows are narrow and shallow. The posterior borders are narrow adaxially, widening abaxially toward the genal angles. In the middle, the posterior borders swell quite strongly while toward both the adaxial and abaxial ends they are flatter. At the genal angles the posterior borders are widest and meet the lateral borders which are also widest here and narrowing gradually forward. The cephalon lacks the ventral parts as well as the anterior border.

The eyes are small with oval outlines. The palpebral furrows are shallow, narrow and adaxially curved. The palpebral lobes are weakly swollen and crescentic in shape with their outer margin irregularly curved adaxially. They are wide medially, narrowing both posteriorly and anteriorly where they meet the eye socles. The eye socles are narrow, very weakly swollen, crescentic in shape and curve abaxially. The visual surfaces are approximately oval-shaped with irregular inner and outer margins. The visual surfaces slope steeply and are fitted with 9 lenses arranged in 5 dorsoventral rows (22221). The lenses are small and rounded in outline, the lenses on the lower horizontal row being a little smaller than those on the upper rows.

The surface of the cephalon lacks ornamentation. The internal mould is smooth while the carapace is not very well preserved. There is no mesial tubercle on the occipital ring.

Ontogeny (Plate 11, figure 14b)

The juvenile, probably of late meraspis, differs from the adult in possessing genal spines, a wider glabellar angle (90°) with a straight posterolateral glabellar margin and well marked facial sutures. The preocular branch of the facial suture appears at the anterolateral cephalic margin shortly in front of the lateral glabellar corner and curves abaxially before meeting the ocular branch which is adaxially curved. The postocular branch of the facial suture appears at the rear end of the visual surface and curves anterolaterally toward the lateral cephalic margin in front of the genal angle. The presence of all the branches of the facial suture suggests that it might be functional, even though in the available example the librigenae are in contact with the cranidium. The juvenile is similar to the adult in the configuration of their palpebral lobes, palpebral furrows, occipital and preoccipital rings, genae, border furrows and border region.

Comparison and discussion

The Lounston and German specimens of Cr? ensae are, in most of their features, identical. They all have a wide glabella which is slightly angular laterally, a poorly developed preoccipital ring, a shallow and narrow S1 preoccipital furrow and occipital furrow, a shallow and narrow palpebral furrow and a similar eye shape. Similar shapes of palpebral lobe and visual surface and similar ranges of lens content completes the list of identical features. In comparison to the German specimens, the Lounston examples have slightly deeper axial furrows, narrower eye socles and no mesial tubercle.

Compared to Cr? wocklumeriae lounstonensis n.ssp., the Lounston Cr? ensae has a non-functional facial suture, a poorly developed preoccipital ring, a shallower S1 preoccipital glabellar furrow and occipital furrow, a narrower glabellar angle and a slightly angular lateral glabellar corner.

The presence of the functional facial suture in the juvenile of this species is common in some other phacopid juveniles (see Chlupáč 1977^{i}, p.128). The possible functional facial suture in the juvenile of Cr? ensae of Lounston could be a new characteristic feature for this species, from which no juvenile has previously been described.

2.4.3 Cryphops sp.A.

(Plate 2, fig.16)

Locality: Sublocality 1D of the Lounston fossil band (see text-figure 1.2b, p.6)

Horizon: The Rora Slate - *sphaeroides* subzone (≡ Zone VIβ of the Famennian).

Materials: 1 partly complete specimen (cephalon without librigenae and ventral parts with pygidum and parts of thorax). Specimen No. AD 1868/9 held in the I.G.S. Museum, London.

Description

A small trilobite with a sagittal cephalic length of 3.7mm. Its cephalic outline less the posterior margin is longer than semicircular. The genal angles are rounded and parabolic. The posterior cephalic margin is almost straight. In front view the glabella is convex, as are the genae. In side view the glabella gradually inclines forward from its summit which is situated at the rear end of the frontal glabellar lobe. The anterior glabellar margin is thin and overhanging, but the anterior border cannot be detected since it was probably shed together with the librigenae during moulting. The preoccipital ring is lower than both the frontal glabellar lobe and the occipital ring.

The frontal glabellar lobe is large, and expands strongly forward with straight posterolateral margins. The glabellar angle is 65°, and remains constant from its entrant angle posteriorly to the lateral glabellar corner anteriorly. The lateral glabellar corners are slightly angular. The anterior glabellar margin is smoothly curved forward. The S2 and S3 glabellar furrows are absent. The S1 preoccipital glabellar furrow is narrow and shallow, continuous and quite strongly curved forward medially. The lateral preoccipital pits are deep, wide and transversely elongated. The preoccipital ring is narrow, short, low and unobtrusive. The median and the lateral lobes are only separated by a shallow depression. The occipital furrow is shallow and narrow, continuous and weakly curved forward medially. The occipital ring is obtrusive and slightly longer and wider than the preoccipital ring.

The axial furrows are wide and deep, continuous posteriorly. The genae are small, quite inflated and equilaterally triangular in shape. The librigenae and the eye are missing due to moulting. The facial suture is functional and is represented by a smoothly curving postocular branch, although its ocular and preocular branches cannot be seen due to the broken lateral margin of the cranidium. The border furrows are narrow and deep. The border areas are generally narrow and swollen, widest at the genal angles with the lateral borders gradually narrowing forward before being cut by the facial suture while the posterior border narrows continuously adaxially to the occipital ring. The remaining palpebral lobes are very small in size compared to the genae. They are very weakly swollen; their inner margin bounded by the palpebral furrows which are very shallow and narrow, and adaxially curved while their outer margins are broken. The surface of the cephalon is very weakly granulated and almost smooth.

The thorax is similar to that of other phacopids, the surface of the thorax being smooth as it is in Dianops.

The pygidium is similar to pygidia of other species of Cryphops. It is small with its sagittal length to maximum width ratio at 0.5. The axis bears 3 rings anteriorly, while posteriorly the terminal piece is long, and unlike other Cryphops, is quite sharply pointed backward. The postaxial region and the rear end of the terminal piece are fused together. The axial furrows are narrow and deep anteriorly, shallow backward and become obscure posteriorly. The pleural region has 3 pairs of pleural furrows, marking the presence of 3 pairs of ribs. The interpleural furrow and the border furrow are absent. The border region is marked by a smooth band at the pygidial margin. The surface of pygidium is very weakly granulated and almost smooth.

Comparison and discussion

This species differs from other species of *Cryphops* in having a considerably longer cephalon, the sagittal cephalic length being about 0.7 of the maximum cephalic width, this ratio is smaller in other species of *Cryphops*. Compared with other species of *Cryphops*, this species has a larger glabella, smaller genae, narrower lateral borders and a smoother surface of the cephalon. It also has a functional facial suture, while in other species of *Cryphops* (except *Cr*? *wocklumeriae lounstonensis*), the facial suture is non-functional. The pygidium of this species is longer than in other *Cryphops* species, the sagittal length of the pygidium of this species is half its maximum width while the sagittal pygidial length of other *Cryphops* species is usually far less than half of its maximum width. The surface of the pygidium of this species, like its cephalon and thorax, is smoother than that of other *Cryphops* species.

This species is assigned to genus *Cryphops* because of its similarity to other species of that genus in the profile of the glabella, the size of the palpebral lobes which reflects the size of the eye, the course of the palpebral furrows and the number of rings and ribs on its pygidium.

A bigger and more representative sample is needed before its differences from other Cryphops species can be put on a formal basis.

2.4.4 ?Cryphops? wocklumeriae lounstonensis n.ssp. (pygidium)

Locality: Locality 1A of the Lounston fossil band (see text-figure 1.2b, p.5f).

Horizon: The Rora Slate - sphaeroides subzone (≡ Zone VI of the Famennian) diagnosed by the presence of Epiwocklumeria.

Materials: Specimens Nos. Zo 4642 - 4646 (LC)

Remarks

The pygidium is similar to those of other species of Cryphops. It is small and short with its sagittal length shorter than half its maximum width. The posterior margin is curved weakly rearward. The axis is short, narrow and tapers backward, its length is about the same as its maximum width. The axis has 3 rings and a short terminal piece. The axial furrows deeper anteriorly and shallower posteriorly. The pleural bands bear 2 or 3 pairs of pleural furrows which mark the number of ribs carrying them. The interpleural furrows are absent. The border area is smooth and fused with the pleural region. The postaxial region is very narrow and smooth. The surface of the pygidium is weakly granulated, with very few granules occupying the swollen parts (i.e. rings and ribs) of the pygidium.

These pygidia are similar to those of other species of Cryphops, but since only Cr? wocklumeriae lounstonensis occurs at this locality, the likelihood of them being referable to any other species of Cryphops is low.

Compared with the pygidium of Phacops sp. indet. found at the same location, the pygidium of this species is shorter and has a more weakly curved posterior margin, smaller number of rings and ribs and a smoother surface.

Compared with the pygidium of Dianops sp. indet. from the same location, the pygidium of this species has a bigger number of rings and ribs and a more strongly granulated surface.

2. 5 Genus: Dianops (R. & E. Richter 1923)

* 1926: Phacops (subgenus Dianops) R. & E. Richter; R. & E. Richter pp. 184-190

1955: Dianops R. & E. Richter; Maksimova pp.168-169, text-fig. 30.

1955: Dianops R. & E. Richter; Hupe, p.258, text-fig.224.4.

1959: Dianops R. & E. Richter; Struve in Harrington et al, p.364 text-fig.364E, 365(2a-c).

1966: Dianops R. & E. Richter; Chlupáč, pp.112-113.

1975: Dianops R. & E. Richter; G. & R. Hahn, p.26, pl.2, fig.4.

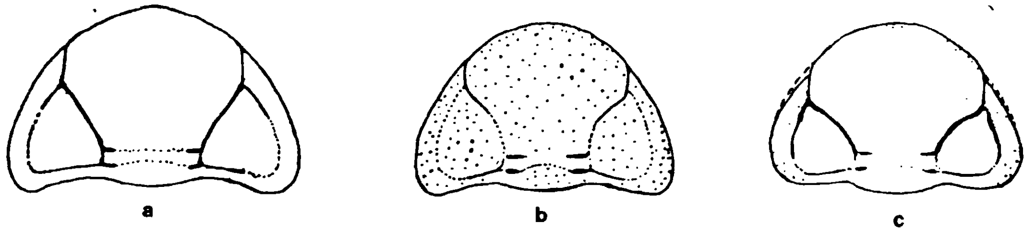
1977: Dianops R. & E. Richter; Chlupáč p.124.

Type species: Phacops limbatus Reinh. Richter 1848, Upper Devonian (Famennian), Thuringia.

Age: Zone IV to VI of the Upper Devonian (Famennian).

Remarks

During the recent research the present author has found a secondary eye on one of the species of Dianops, that is, Dianops tripartitus (Ivor Thomas 1909). This species has been twice put into the wrong genus, Trimerocephalus by Thomas (1909) and Cryphops by R. & E. Richter (1926). Both authors agree on the presence of the eyes in this species. Recently, the type of this species has been restudied and the present author found that this species, in fact, belongs to the genus *Dianops*. Its glabellar construction, the preoccipital ring construction, the configuration of the S1 preoccipital glabellar furrow and the facial suture undoubtedly place it in the genus *Dianops*. The eye projections possessed by this species are, in fact, secondary features, where they are situated on the fixigena instead of on the librigena as in other phacopids. The palpebral lobe, visual surface and the eye socle cannot be distinguished. This new discovery means that a new diagnosis is required for this genus.



a = *D. limbatus* (Reinhard Richter 1848) after G. & R. Hahn (1975)

b = *D. griffithides griffithides* (R. & E. Richter 1919) after G. & R. Hahn (1975)

c = D. tripartitus (Thomas 1909), Zo 4603 x5

Text-figure 2.5 Reconstruction of plan views of the studied *Dianops* found in the Lounston fossil band.

Emended diagnosis

(Modified from the latest diagnosis by Chlupáč, 1977)

Glabella considerably inflated, gently overhanging or steeply falling into anterior border furrow; lateral glabellar corner truncated. Glabellar furrows S2 and S3 very weak (often imperceptible), S1 preoccipital glabellar furrow interrupted or strongly shallowing medially. Preoccipital ring flat, lateral preoccipital lobe not differentiated by vaulting. Axial furrows bent adaxially. Eyes absent except in *D. tripartitus* (Thomas 1909) where there are very small eye projections bearing 1 or 2 rounded lenses and where the palpebral lobe and eye socle are indistinguishable. Facial suture restricted to the borders, functional in some species sheds the anterior border together with the librigenae during moulting. Vincular furrow broad and deep, continuous medially, delimited by ridges (anterior higher than posterior). Anterior border convex ventrally, anterior doublure short. Dorsal surface of the cephalon smooth or finely granulated. Pygidium short and wide, transversely vaulted, its anterior margin angular, posterior margin slightly curved; axial furrows shallow, segmentation weak or indistinct; posterior end of the pygidium smooth (all furrows totally diminished).

2.5.1 *Dianops limbatus* (Reinh. Richter, 1858)

(Plate 4, figs. 7-9, text-fig. 2.5a, p.58).

1926: *Phacops* (*Dianops*) *limbatus* (Reinh.Richter); R. & E. Richter, pp.190-191, pl.10, figs. 87-89.

1936: *Phacops* (*Dianops*) *limbatus* (Reinh.Richter); Stubblefield, text-fig. 5e.

1954: *Phacops* (*Dianops*) *limbatus* (Reinh.Richter); Pfeiffer, pp.45-45, pl.3, figs.1-4.

1959: *Dianops limbatus* (Reinh.Richter); Struve in Harrington *et al*, text-fig.352 (2a,2b).

1975: *Dianops limbatus* (Reinh.Richter); G. & R. Hahn, p.26, pl.2, fig.14.

Locality: Localities 1A and 1C of the Lounston fossil band (see text-fig. 1.2b, p.5f) and locality 10 (see text-fig. 1.2a, p.5f).

Horizon: The Rora Slate - *sphaeroides* subzone (≡ Zone VIβ of the Famennian) diagnosed by the presence of *Epiwocklumeria*. The age of the locality 10 is uncertain (no critical index fossil found).

Materials: From locality 1A - specimens nos. Zo 4617-4621(LC), Zo 4622 (BC) & AD 1904 (WC).

From locality 1C - specimen no. Zo 4671 (LC).

From locality 10 - specimen no. AD 2183(4 (WC)

Preservation: Condition of preservation is not very good.

Diagnosis

Cephalon longer than semicircular, slightly angular anteriorly. Posterior margin weakly curved forward. Genal angle rounded and parabolic. Glabella wide, quite inflated with an inequiheptagonal shape; posterolateral glabellar margin almost straight, lateral glabellar corner truncated and anterior margin slightly angular. Glabellar angle wide. Preoccipital ring poorly developed, fused medially with frontal glabellar lobe and occipital ring; S1 preoccipital glabellar furrow and occipital furrow are indistinct while their lateral pits are shallow, narrow and laterally elongated. Axial furrows narrow and shallow. Border furrows are very shallow and almost interrupted at the genal angle. Facial suture absent.

Description

Small trilobites with sagittal cephalic lengths ranging from 5.0mm to 9.4mm. The cephalic outline is longer than semicircular. The anterior cephalic margin curves smoothly anterolaterally, slightly angular anteriorly. The genal angles are smoothly rounded and parabolic. The posterior margin of the cephalon is weakly curved forward. The glabella and genae are convex in front view, the latter continuously sloping abaxially to the lateral borders which form a less steep slope than that of the genae. In side view the highest point of the cephalon is situated at about one quarter of the frontal glabellar lobe in front of its posterior base. From this summit the glabella slopes steadily forward to the thin and overhanging anterior glabellar margin, and rearward the glabella slopes steadily to the low and unobtrusive preoccipital ring. The occipital ring is quite obtrusive.

The glabella is large, weakly inflated and expands strongly forward. The glabellar angle ranges from 77° to 85°. The outline of the glabella forms an inequiheptagonal shape. The posterolateral glabellarmargins are short, straight, or only weakly bend outward. The lateral glabellar corners are abruptly truncated with both sides almost parallel to each other, the exosagittal length of the truncated lateral glabellar corner being about one third of the sagittal length of the frontal glabellar lobe. Widest at its truncated lateral corner, the glabellar broadly tapers forward forming an angle of about 120° at its posterior extremity. Sometimes the anterior glabellar margin is smoothly although weakly curved forward. The S2 and S3 glabellar furrows are absent. The S1 preoccipital glabellar furrow and the occipital furrow are indistinct so that the preoccipital ring is fused with the frontal glabellar lobe and occipital ring medially. Laterally the preoccipital ring is separated from the frontal glabellar lobe anteriorly and the occipital ring posteriorly by the narrow, shallow and transversely elongated lateral preoccipital and occipital pits respectively. The median part of the preoccipital ring forms a low depression while the lateral parts of it form ridges which are higher abaxially and lower adaxially. The occipital ring is narrow, short and obtrusive and usually has a biconvex shape.

The axial furrows are narrow and shallow; deepest anteriorly, shallowing gradually toward the rear end. The genae are quite inflated and slope steeply abaxially to the lateral borders which are almost inseparable from the genae. The lateral border furrows are very shallow and narrow, shallowest and almost interrupted at the genal angle where they meet the posterior border furrows which are shallow abaxially, deeper adaxially. The posterior borders are narrow adaxially, widening abaxially toward the genal angles. At the genal angles the lateral borders are widest, narrowing gradually forward. The posterior borders are slightly swollen while the lateral borders are almost flat. There are no eyes, no facial sutures and no librigenae on the dorsal part of the cephalon. The cephalon lacks the ventral parts.

The surface of the cephalon is smooth.

Compressional damage

Due to strong compression the flattened specimens show some differences which might confuse observers. On the more compressed specimens the genae become strongly flattened; the genal angles become angular and the lateral borders become extremely wide. The lateral glabellar corners are no longer parallel to each other. The preoccipital ring becomes very low so that the frontal glabellar lobe drops vertically to it; the lateral occipital and preoccipital pits become rounded and the occipital and preoccipital rings become very narrow.

Comparison and discussion

The less compressed specimens of Dianops limbatus from Lounston (Plate 4, fig. 7) are very similar to the reconstructed figures of the holotype of this species from Germany (see Struve in Harrington et al (1959) and G. & R. Hahn (1975). Their main differences lie in the absence of the facial sutures in the Lounston examples, present in the German specimens. This apart, all other differences are those of relative size variations in the dorsal cephalic components. The Lounston examples have a slightly wider glabella, narrower occipital and preoccipital rings, and wider genae than that of the German examples. Other features are very similar.

The Lounston examples of D. limbatus are easily distinguishable from other species of Dianops. Dianops griffithides (R. & E. Richter 1919) resembles D. limbatus of Lounston in having a truncated lateral glabellar corner, narrow and shallow axial furrows and a poorly developed preoccipital ring but in comparison to the latter, D. griffithides has a smaller glabella with strongly bent posterolateral glabellar margins and a smoothly curved anterior margin, very poorly developed lateral borders and a granulated surface to the cephalon. The compressed specimens of D. limbatus are more difficult to distinguish from D. griffithides since they sometimes have a smoothly curved anterior glabellar margin, strongly bent posterolateral glabellar margins and poorly developed lateral border furrows, but the former differs from D. griffithides in having a bigger glabella and a smoother surface of the cephalon.

Remarks on palaeogeographical distribution

D. limbatus until recently has never been found outside its original site, that is, East Germany (Thuringen-Frankenwald area). The recently found member of this species in the South West of England reveals a very interesting aspect of palaeogeography. Having the longest age range (Zone IV to VI of the Famennian) among the Dianops, this species must have found a migration route from East Germany to England.

The absence of this species from the area between East Germany and England is not fully understood, and certainly no conclusions can be drawn to its overall distribution until the concealed Upper Famennian in Northern France and South-eastern England has been explored.

2.5.2 Dianops griffithides griffithides (R. & E. Richter 1919)

(Plate 3, figs. 9-12, text-fig. 2.5b, p.   )

1926: Phacops (Dianops)griffithides (R. & E. Richter); R. & E. Richter, pp.197-199, pl.11, figs. 1-9.

1936: Phacops (Dianops)griffithides (R. & E. Richter); Stubblefield, text-fig. 5f.

1955: Dianops aff. griffithides (R. & E. Richter); Maksimova, pp. 178-179, pl.16, fig.17.

1975: D. griffithides griffithides (R. & E. Richter); G. & R. Hahn, p.26, pl.2, fig.16.

Localities: Lounston fossil band (from all sublocalities) (see text-fig. 1.2b, p.5f).

Horizons: The Rora Slate, sphaeroides subzone ($\equiv$ Zone VIβ of the Famennian) diagnosed by the presence of Epiwocklumeria.

Materials: From locality 1A - specimens nos. Zo 4611-4612, 4614-4616, 4654 & HMA 21151(LC).

From locality 1D - specimen no. AD 1869 (WC).

From locality 1B - specimen no. Zo 4680 (LC).

From locality 1C - specimens nos. Zo 4663-4670 (LC).

Conditions: Generally the condition of preservation is fairly good.

Diagnosis

Cephalic outline longer than semicircular; anterior margin weakly curved forward. Genal angle rounded and parabolic. Posterior cephalic margin weakly curved forward. Glabella convex and inflated; posterolateral glabellar margins strongly bend outward anteriorly; lateral glabellar corner truncated. S1 preoccipital glabellar furrow and occipital furrow interrupted medially, their lateral pits transversely elongated. Preoccipital ring flat, and unobtrusive medially, ridged laterally. Axial furrows narrow and shallow, interrupted at the genal angle. Posterior borders weakly swollen; lateral borders flat. Surface of cephalon well granulated. Thorax and pygidium similar to other species of Dianops.

Description

Small to relatively large trilobites with sagittal cephalic lengths ranging from 1.6mm to 14.2mm. The cephalic outline, less the posterior margin is longer than semicircular with anterior margins smoothly curved forward. The genal angles are well rounded and parabolic (never stronger than parabola $4y=x^2$). The posterior cephalic margin is weakly curved forward. In front view the glabella and the genae are convex, more strongly so in the former. The genae slope steadily and continuously as far as the lateral cephalic margin. In side view the profile is quite low; the glabellar summit being situated slightly in front of the preoccipital ring. From its summit, the glabella slopes weakly forward, but the slope gradually becomes steeper as it approaches the anterior glabellar margin. The anterior glabellar margin is thin and overhanging. From its summit rearward the glabella slopes steeply toward the low and unobtrusive preoccipital ring. The occipital ring is quite obtrusive.

The glabella is inflated, medium in size and weakly expanding forward. The glabellar angle is narrow posteriorly (45^{0} to 65^{0}) but this angle widens strongly anteriorly (80^{0} to 100^{0}) before it reaches the lateral glabellar corners. The lateral glabellar corners are truncated with both sides parallel to each other. The anterior glabellar margin is weakly curved forward. The S2 and S3 glabellar furrows are absent. The S1 preoccipital glabellar furrow is straight, very shallow and narrow laterally, interrupted medially. The lateral preoccipital and occipital pits are narrow, deep and transversely elongated, the former being slightly longer than the latter. The preoccipital ring is narrow and short, low and flat medially; lateral preoccipital lobes form ridges, wider and higher abaxially, narrow and low adaxially. The occipital furrow curves forward, is narrow and shallow laterally, shallower and almost indistinct medially. The occipital ring is inflated, narrow, short and biconvex in shape.

The axial furrows are shallow and narrow, deeper anteriorly, shallow posteriorly especially in between the preoccipital ring and the genae. The genae are inflated and poorly defined especially laterally and beside the preoccipital ring. The genae slope almost continuously to the lateral cephalic margin. The lateral border furrows are only indicated by a shallow depression anteriorly while posteriorly the furrows are interrupted at the genal angle. The posterior border furrows are deep and narrow adaxially, shallowing abaxially and fading away before reaching the genal angle. The posterior borders are narrow and slightly swollen adaxially, widening and flattening abaxially toward the genal angles. At the genal angles the posterior borders meet the lateral borders, the latter having a maximum width here, narrowing gradually forward. The lateral borders are flat. There is no facial suture, librigenae or eyes. The cephalon lacks detail on its ventral parts. The surface of the cephalon is well granulated with fine hemispherical granules (diameter less than 0.05mm) which are closely packed and evenly distributed all over the cephalon. The cephalic granulation is best exhibited by the external moulds while the carapaces occasionally lack granulation. The internal moulds are smooth.

The thorax has a wide and obtrusive axial ring, very shallow axial furrows and no axial nodes. The pleural furrows are deep and narrow, restricted to the inner half of the pleurae. The outer half of the pleurae bend posteriorly and ventrally. The pleural ends are rounded. The surface of the thorax is almost smooth.

The pygidium is short and wide. The posterior margin is almost straight (very weakly curved rearward) while the anterior margin is angular. The axial ring is wide anteriorly, tapering rearward but indistinguishable from the pleural bands and the post-axial region posteriorly. 2 weakly swollen rings can be recognised anteriorly, they are separated by narrow and shallow ring furrows from each other. The axial furrows are quite deep anteriorly, rapidly shallowing rearward and fading away posteriorly. On the pleural region 2 pairs of ribs can be recognised anteriorly, marked by the presence of 2 pairs of pleural furrows which are narrow and shallow. the interpleural furrow and border furrow are absent. The border region is fused with the pleural region laterally and the axial ring posteriorly. The surface of the pygidium is almost smooth.

Ontogeny

a. Juvenility. Specimens with sagittal cephalic lengths of less than 2.1mm (probably slightly bigger because the smallest holaspids available have a cephalic length of 4.2mm) considered to be juveniles, probably of the late meraspid stage. However lack of details on the number of thoracic segments made it impossible to recognise the exact ontogenetic stage. The juvenile has a pair of genal spines and functional facial sutures, these being absent in the adult specimens. Furthermore the juvenile differs from the adult in having a narrower glabellar angle posteriorly, a more inflated glabella and genae, deeper axial furrows, clearer border furrows (uninterrupted at the genal angle) a straighter posterior cephalic margin and a smoother cephalic surface.

b. ?Senility. Besides the juvenile, the larger adults also show some variation from the above standard description. The two largest adults with sagittal cephalic lengths larger than 8.5mm show some minor changes in the configuration of the glabella, axial furrows and lateral border furrows. The glabella of the larger adults compared to the smaller ones is flatter and relatively smaller with shorter posterolateral margins, longer and well truncated lateral corners and a more weakly curving anterior margin (almost straight anteriorly). The axial furrows are deeper and the lateral border furrows are slightly clearer in the larger adult than that of the smaller one. The environment in which the specimens were preserved offers the possibility that these morphological changes in the larger specimens are due to deformation since they are more exposed to this process than are the smaller specimens. However, the relatively smaller glabellar size, the deeper axial furrows and the clearer lateral border furrows are unlikely to result from compressional damage. On flattening, the shape of the glabella might be changed, but the size of the glabella should be larger instead of smaller, the axial furrows should be shallower instead of deeper and the lateral border furrows should have faded away instead of becoming clearer. Compared to the undeformed examples these differences might be a property of the gerontic (senile) stage of the species, although a collection of large adults from undeformed rocks might be useful to prove the presence of gerontic characteristics in this species.

Comparison and discussion

Except for minor differences in the glabella and the preoccipital ring the Lounston and German examples of *Dianops griffithides griffithides* are very similar. The glabella of the Lounston specimens is slightly shorter and wider than that of the German specimens. The glabella of the German specimen has only slightly truncated lateral corners and a more strongly curved anterior margin than the Lounston one. The preoccipital ring of the German specimens is slightly higher than that of the Lounston specimens. In other features they are very similar.

D. griffithides griffithides both from Lounston and from Germany, can be easily distinguished from other species of *Dianops* by their strongly bent posteriolateral glabellar margin, very faint lateral border furrows and the strongly granulated surface of the cephalon.

Dianops tripartitus (Thomas) having a similarly strongly bent posterolateral glabellar margin differs from *D. griffithides griffithides* by having more strongly marked lateral border furrows, a bigger glabella and a smoother cephalic surface. Furthermore *D. tripartitus* possesses secondary eyes and functional facial sutures.

D. limbatus may have a shallow and very weakly developed lateral border furrow but, *D. griffithides griffithides* can be distinguished from the former by its strongly bent posterolateral glabellar margins, less well truncated lateral glabellar corners and a strongly granulated surface.

Other species of *Dianops* differ considerably from *D. griffithides griffithides*.

2.5.3 *Dianops tripartitus* (Thomas 1909)

(Plate 4, figs. 1-6, text-fig. 2.5c, p. 58)

* 1909: *Phacops* (*Trimerocephalus*) *tripartitus* Thomas; p.196, pl. 7, figs.4-5 (specimens nos. 22884/23431 - in the Museum of Practical Geology, London).

non 1909: *Phacops* (*Trimerocephalus*) *tripartitus* Thomas; not figured (specimen no. US 1717 in the Museum of Practical Geology, London

? 1909 *Phacops* (*Trimerocephalus*) *tripartitus* Thomas; not figured, (specimen no. US 1722 in the Museum of Practical Geology, London).

1926: *Phacops* (*Cryphops*) *tripartitus* (Thomas); R. & E. Richter; p.168 (specimen nos. 22884/23431 in the Museum of Practical Geology, London).

non 1926: *Phacops* (*Cryphops*) *tripartitus* (Thomas); R. & E. Richter; p.168 (specimen no. 22884 Thomas's *Ph.*(*Tr.*) aff. *cryptophthalmus* in the Museum of Practical Geology, London.

Localities: Localities 1A, 1D and 1C of the Lounston fossil band (see text-fig. 1.2b, p.5f) and Whiteway Farm, Ideford.

Horizons: The Rora Slate - *sphaeroides* subzone (≡ Zone VIβ of the Famennian) diagnosed by the presence of *Epiwocklumeria*.

Materials: From locality 1A - Specimens nos Zo 4602-4608 (LC), Zo 4610 (BC).

From locality 1D - Specimens nos AD 1861/3 (WC)

From locality 1C - Specimens nos AD 4660-4662 (LC)

From Ideford (Whiteway Farm) - Specimens nos 22884/23431, US 1717 and US 1723 (Ussher's collection)

Condition: Generally condition of preservation is good.

Diagnosis

Cephalic outline is longer than semicircular with smoothly curved anterior margin, genal angle rounded but not always parabolic. Posterior outline almost straight. Glabella is large, inflated and convex, strongly expanding forward from a very narrow preoccipital ring. Glabellar angle ranges from 70° - 80° at the entrant angle; the posterolateral glabellar margins bend outward toward the truncated lateral glabellar corners. Anterior glabellar margin curved forward. Preoccipital ring poorly developed, low and unobtrusive. S1 preoccipital glabellar and occipital furrows very shallow and indistinct. Lateral occipital and preoccipital pits deep, circular in outline.

Occipital ring quite obtrusive. Axial furrows narrow and quite deep. Genae small with very small eye projections on their anterolateral corners. The eye projections are secondary features, either bearing visual surfaces with one or two lenses or no visual surface at all. The facial suture is functional and restricted to the lateral border. Lateral border furrows narrow and shallow. Lateral border narrow, widest slightly in front of the genal angle. Vincular furrow deep and wide anteriorly, narrowing laterally. Surface of the cephalon smooth or very poorly granulated.

Description

Small trilobites with sagittal cephalic lengths ranging from 3.0mm to 7.9mm. The cephalic outline less the posterior margin is longer than semicircular, smoothly curved anteriorly, the curve fitting any range from a parabola $2y=x^2$ to semicircular. The maximum width occurs slightly in front of the genal angle, the lateral borders being widest here instead of at the genal angles. The genal angles are smoothly rounded but not always parabolic. The posterior cephalic margin is almost straight. In front view the glabella is convex, as are the genae. The genae slope very gently to the lateral border furrows which are very faintly marked, separating the lateral borders from the genae. In side view the profile is low and the glabella summit is situated at approximately one third of the glabellar length in front of the rear end of the frontal glabellar lobe. From the summit, the glabella slopes gradually forward to the anterior glabellar margin. From the summit rearward the glabella slopes steeply to the low and unobtrusive pre-occipital ring. The occipital ring is obtrusive. The genae are weakly inflated, less so than the glabella and the occipital ring.

The posterior border is slightly swollen.

The glabella is weakly inflated, wide and expands quite strongly forward from a narrow preoccipital ring. The glabellar angle at its entrant angle ranges from 70° to 80°, the posterolateral glabellar margins bend quite strongly outward, widening the glabellar angle anteriorly. The lateral glabellar corners are truncated with both sides parallel to each other, the exosagittal length of the truncated lateral glabellar corners ranges from a quarter to one third of the sagittal length of the frontal glabellar lobe. The posterior end of the lateral glabellar corners are strongly overhanging while anteriorly they overhang less strongly or sometimes drop vertically to the lateral borders. At the truncated margin the glabellar is at its maximum width which is usually more than twice the width of the preoccipital ring. The anterior glabellar margin is short and curves smoothly but weakly forward. The S2 and S3 glabellar furrows are absent. The S1 preoccipital glabellar furrow is straight, very narrow and shallow and interrupted medially. The lateral preoccipital and occipital pits are deep and almost circular in outline or sometimes very slightly transversely elongated. The preoccipital ring is low, unobtrusive and fused medially with the frontal glabellar lobe and the occipital ring. Laterally the preoccipital ring forms ridges which are transversely elongated, higher abaxially and lower medially. The preoccipital ring is separated laterally from the genae only by shallow depressions. The occipital furrow is narrow, shallow and curves forward, but is interrupted medially. The occipital ring is short and narrow but slightly longer and wider than the preoccipital ring; it is quite inflated and has a slightly biconvex shape.

The axial furrows are narrow and deep at their anteriormost extremities and shallower posteriorly being very shallow between the preoccipital ring and the genae. The genae are small, less inflated than the glabella and occipital ring, gently sloping abaxially toward the lateral cephalic margin and interrupted slightly at the border furrows. Small eye projections protrude from the anterolateral corners of the genae, overhang anteriorly.

Small eye projections are found on the anterolateral corners of the genae, at the position where the primary eye might be expected. These eye projections sometimes carry visual surfaces with one or two small (diameter around 0.05mm) and rounded lenses or sometimes do not carry any visual surface. These eye projections are secondary features where the facial sutures do not run through them as in other sighted phacopids. The palpebral furrow, palpebrallobe and eye socle cannot be distinguished on these eye projections.

The lateral border furrows are shallow and narrow, shallowest at the genal angles. The posterior border furrows which are shallowest when they meet the lateral border furrows at the genal angle, deepen considerably adaxially. The posterior borders are narrow and swollen adaxially, wider and flatter abaxially. The lateral borders are widest slightly in front of the genal angle, narrowing gradually anteriorly; they are weakly swollen at the genal angle and flatten anteriorly.

The facial suture is functional and restricted to the border laterally and crosses the glabella anteriorly. On the dorsal cephalon the presence of the functional facial suture is almost unnoticeable because the librigenae are very narrow in front view. The facial suture forms a straight line, springs from the lateral cephalic margin slightly rearward of the position of the eye, continuous on the lateral border (along the cephalic margin) forward. At the anterior end of the lateral glabellar corners the facial suture crosses the anterior border furrows to the base of the glabella and is continuous medially along the base of the glabella. In the moulting processes the base of the anterior glabellar margin is shed together with the very narrow librigenae, anterior border and the ventral parts. The anterior border furrow is very narrow and shallow. The anterior border is short and swollen, the anterior doublure is very short and inseparable from the anterior border. The vincular furrow is wide and deep medially, narrowing laterally and continuous along the lateral cephalic margin.

The surface of the cephalon is smooth or only very finely granulated.

Ontogeny

The juveniles with sagittal cephalic lengths of less than 3.2mm, when compared to the adult reveal some different characters. These juveniles are of late meraspid age (the exact juvenile stage cannot be determined without details of the thoracic segments). The juvenile in comparison to the adult has a narrower glabellar angle, a more convex and inflated glabella and genae and a pair of genal spines. In other respects the juveniles of this species are very similar to their adults.

Remarks

In its latest development R. & E. Richter (1926) this species was assigned to the genus Cryphops. However, this species, despite having an eye or eye-like projection (in the case where lenses are absent), is morphologically much closer to the genus Dianops than the genus Cryphops (see Richter 1926, p.168). Among the diagnostic features of this species which belong to the genus Dianops but differ from the genus Cryphops are:

1. The glabella - The lateral glabellar corner truncated. The glabella summit situated in the middle of the glabella (not at the rear end of the glabella as in Cryphops).
2. The S1 preoccipital glabellar furrow is shallow, discontinuous and straight medially (instead of curving forward as in Cryphops). The occipital furrow is also shallow and interrupted medially (continuous in Cryphops).
3. The configuration of the preoccipital ring - The median part not being lobed (lobed in Cryphops).
4. The facial suture is restricted to the border laterally (instead of crossing the lateral border furrow and separating the visual surface from the palpebral lobe).
5. The vincular furrow is wider and deeper medially than in any Cryphops.
6. Sculpture - The surface of the cephalon is almost smooth (while Cryphops usually has a very well granulated surface).
7. The eye - The eyes of this species are secondary, the palpebral lobe and palpebral furrow cannot be distinguished. Furthermore, the facial suture does not run through the eye like those of Cryphops.
8. The thorax - There is no difference between the thorax of this species and that of Cryphops except that the thoracic surface of this species is smoother than that of Cryphops.

These great differences between this species and Cryphops contrast strongly with the Richters' (1926) description. In contrast, the similarities between this species and other species of Dianops undoubtedly enable it to be referred to this genus. However the presence of a new feature (i.e. the eye) in D. tripartitus requires a new revision on this genus (see p. 58).

Comparison and discussion

The species closest to D. tripartitus are D. anophthalmus (Frech 1892) and D. limbatus (Reinh. Richter 1848). D. anophthalmus resembles D. tripartitus in having a narrow occipital ring and preoccipital ring and a relatively deep and wide axial furrow. However D. anophthalmus differs from D. tripartitus in having a longer cephalon, with a smaller glabella, a narrower glabellar angle, a very weakly truncated lateral glabellar corner and a strongly curving anterior margin. Furthermore the posterior cephalic margin of D. anophthalmus is always curved anteriorly compared to the straight margin of D. tripartitus. D. anophthalmus does not have an eye and a functional facial suture.

D. limbatus of this study, seen both in Lounston and Germany, resembles D. tripartitus in having a large glabella with long, truncated lateral glabellar corners. It differs in having slightly wider occipital and preoccipital rings, narrower axial furrows, weaker border furrows and a narrower and flatter lateral border. Furthermore D. limbatus has a less strongly curved posterolateral glabellar margin and a slightly angular anterior glabellar margin when compared to D. tripartitus. D. limbatus does not have an eye and a functional facial suture.

D. griffithides griffithides resembles this species in having a strongly curved posterolateral glabellar margin but differs from it in having a smaller glabella, weaker and interrupted lateral border furrows, a better granulated cephalic surface, a nonfunctional facial suture and no eye. (see p. 67).

D. tripartitus is easily distinguished from all other remaining species of Dianops in having a large glabella which is strongly truncated and rapidly expands forward, narrow occipital and preoccipital rings, narrow lateral borders, eyes and a functional facial suture.

Comments on type species and earlier descriptions

Difficulties arise when the holotype material of D. tripartitus is considered, for Thomas's original description (Thomas, 1909, p.196) was based on specimen 22884 (fig.4 of Thomas, 1909) which the present author has found to be a juvenile since it bears distinct genal spines. In all, Thomas cited 4 specimens numbered as 2284, 23431, US 1717 and US 1722 all held in the Museum of Practical Geology, London. Thomas's specimens must now be redesignated and redistributed to 3 since specimen no. 23431 (fig.5 of Thomas, 1909) is in fact a counterpart of specimen no. 22884. The specimen no. US 1717 on the other hand, is a genuine juvenile of Cryphops diagnosed by its strongly convex and inflated glabella with a straighter posterolateral margin and rounded lateral corners, distinct S1 preoccipital glabellar and occipital furrows, lobed median preoccipital ring, inflated occipital ring and genae, quite deep lateral border furrows and a swollen lateral border. It bears genal spines. Although its eye is absent and the granulation is not very well preserved, the other features are very closely similar to Cr? wocklumeriae. Finally, the largest specimen (no. US 1722) although it is an example of Dianops is specifically indeterminate due to damage.

→
Plate IV
Plate V

EXPLANATION OF PLATE IV

1-6. *Dianops tripartitus* (Thomas 1909).

1-4, 6. Locality 1A (Lounston fossil band)(LC); 5 - Whiteway Farm Ideford, Chudleigh. (Thomas' collection).

1. Zo 4603, internal mould, plan view (x6, coated with ammonium chloride).

2. Zo 4602a,b, latex cast of the external mould (Zo 4602b), plan view (x5, coated with ammonium chloride).

3-4. Zo 4604a,b, internal mould plan view shows the shifted ventral part of the cephalon (4) from the cephalon (3) in the true distance, plan view (x5, coated with ammonium chloride).

5. 22884, internal mould , type specimen; plan view (x5, coated with magnesium oxide).

6. Zo 4605, internal mould, plan view (x5, coated with ammonium chloride).

7-9. *Dianops limbatus* (Reinh. Richter 1848) Locality 1A (Lounston fossil band).

7. AD 1904 (WC), cephalon with part of carapace and internal mould, plan view (x2, coated with ammonium chloride).

8. Zo 4618a (LC), internal mould with secondary granulation, plan view (x5, coated with ammonium chloride).

9. Zo 4617a (LC), internal mould, plan view (x3, coated with ammonium chloride).

10-13. *Dianops combensis* n.sp. Combe fossil band (locality 2) (LC).

10. HOLOTYPE (Zo 4681) shows a "salterian moult" mode of ecdysis, plan view (x3, coated with ammonium chloride).

11. Zo 4690a, side view of compressed complete animal (x3, coated with ammonium chloride).

12. PARATYPE III (Zo 4684); "salterian moult" in normal life position, plan view (x3, coated with ammonium chloride).

13. Zo 4691a, cephalon and hypostome, plan view (x3, coated with ammonium chloride).

PLATE IV

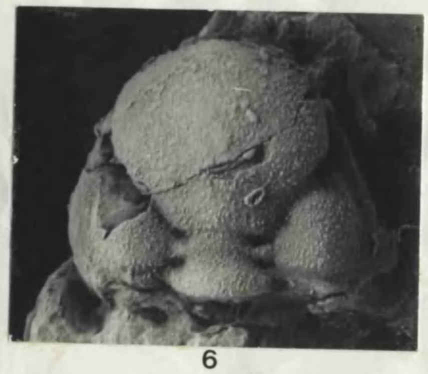

1


2


3


4


5


6


7


8


9


10


11

12

13

EXPLANATION OF PLATE V

Dianops combensis n.sp. Combe fossil band (Locality 2).

1-3 PARATYPE I (Zo 4682), internal mould, plan, front and side view (x3, coated with ammonium chloride).

4-5 PARATYPE II (Zo 4683), internal mould, plan and front view (x3, coated with ammonium chloride).

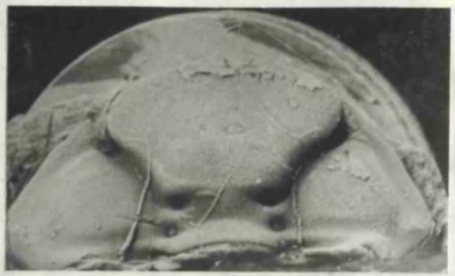
6. Zo 4685 shows detached thorax (post moulting) (x3, coated with ammonium chloride).

7. Zo 4686 shows a disorientated cephalon, plan view (x3, coated with ammonium chloride).

8. Zo 4687 a complete specimen in plan view together with a larger cephalon Zo 4688 (x3, coated with ammonium chloride).

9-10. Zo 4689 internal mould, plan and front view (x3, coated with ammonium chloride).

PLATE V


1


6


2


3


7


4


8


5


9


10

In their (1926) revision, R. & E. Richter expressed some doubt on the validity of Thomas's species and attempted to widen its morphological range by including other phacopid specimens from the same slab of rock as *D. tripartitus*. The addition of these other specimens called *Phacops* (*Trimerocephalus*) aff. *cryptophthalmus* (Emmrich) by Thomas, then prompted the Richters to suggest that *D. tripartitus* (they called it *Phacops* (*Cryphops*) *tripartitus*), might overlap with their species *Cryphops*? *wocklumeriae* and *Cryphops*? *ensae*. The present author believes that *Ph.* (*Tr.*)*cryptophthalmus* of Thomas is, in fact, a variety of *Cryphops*? *ensae* and must be removed from *D. tripartitus*.

Thus only one of the above mentioned specimens (No.22884 and its counterpart No.23431) definitely belongs to *D. tripartitus*. But because this specimen is a juvenile its status as a holotype although not invalid is rendered somewhat doubtful bearing in mind the changes between meraspis and holaspis in phacopids in general, and an adult from the type locality should be found to replace it.

2.5.4 *Dianops combensis*, sp. nov.

(pl.4, figs.10-13, pl.5, figs.1-10, text-fig.2.6 a-f, p.80)

Name derivation: Species name was taken from the name of the nearest farm to the type locality, that is Combe Farm.

Type locality: The Combe fossil band (see text-fig. 1.2, p.5f).

Other localities: Locality 1D of the Lounston fossil band and locality 4 (the Rora Trench)(see text-fig.1.2a, b, p.5f).

Horizons: The Rora Slate - for the Combe fossil band - *Euryomphala* zone (≡ uppermost of the Zone VI of the Famennian) diagnosed by the presence of *Cymaclymenia euryomphala*.

The Lounston fossil band - *sphaeroides* Zone (≡ upper Zone VI of the Famennian) diagnosed by the presence of *Epiwocklumeria*.

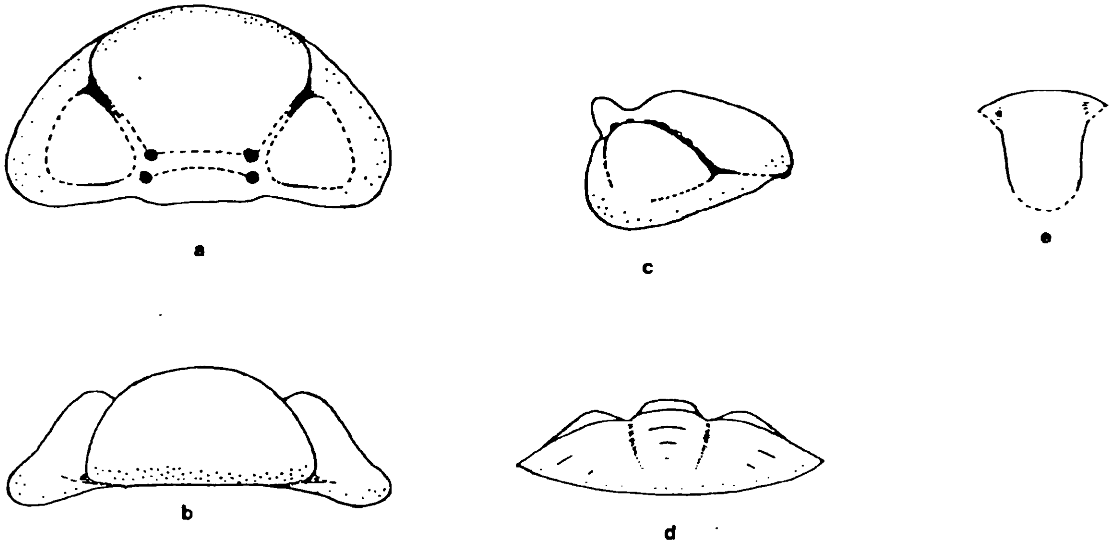
The Rora trench - *hemispherica*-*dichotoma* Zone (Zone V to VI of the Famennian) diagnosed by the presence of *Maternella dichotoma*.

Materials: From Combe fossil band (locality 2) - Specimens Nos Zo 4681-4753, 4757-4807, 4809-4815, 4817-4848 and HMA 21156-21158(LC).

From Locality 1D (Lounston fossil band) - Specimens Nos AD 1877/1878 (WC).

From Rora Trench (locality 4) - Specimens Nos AD 1173, 1174 and 1182 (WC).

Condition: The condition of preservation is fairly good.



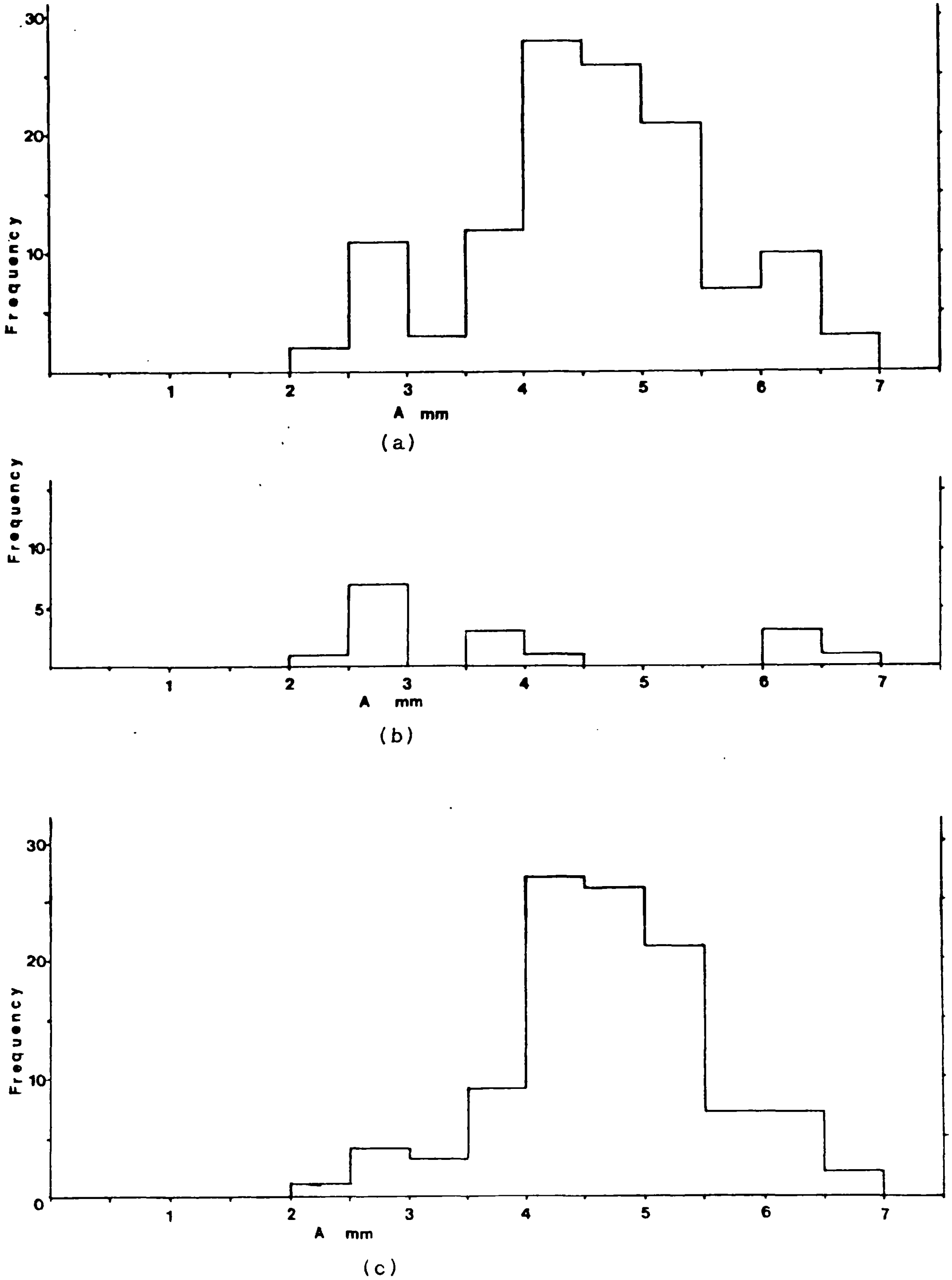
Cephalon: a-c - Paratype I (Zo 4682) x5, plan, front and side (right) view.

Pygidium: d - Paratype III (Zo 4684) x5, plan view.

Hypostome: e - (Zo 4691) x8, plan view.

Text-figure 2.6 Reconstruction of the cephalon, pygidium and hypostome of *D. combensis*, n.sp.

→ Text-figure 2.7



Text-figure 2.7 : Histogram of size frequency distribution for Dianops combensis n.sp. in locality 2

(a) Total observation (b) Dead specimens (c) Moulting activities

.... c=a-b ....

Diagnosis

Cephalic outline only slightly longer than semicircular. Glabella inflated, glabellar angle narrow, posterolateral glabellar margins bend slightly outward; lateral glabellar corner not truncated. S2 and S3 glabellar furrows are absent. S1 preoccipital glabellar furrow and occipital furrow very narrow and shallow, interrupted medially. The lateral occipital and preoccipital pits are circular in the internal mould, laterally elongated on the carapace. Preoccipital ring very low and unobtrusive, median part not lobed. Occipital ring obtrusive. Occipital and preoccipital ring quite wide. Axial furrows wide, deep anteriorly, shallower posteriorly. Genae inflated sloping laterally to the margin almost without interruption of lateral border furrows. Lateral border furrows very shallow and indistinct. Border narrow. Genal angle smoothly rounded and parabolic, sometimes slightly angular. There are no eyes, librigenae or facial sutures. Anterior border inseparable from anterior glabellar margin anteriorly and anterior doublure posteriorly, narrow and swollen. Vincular furrow wide and deep medially, narrows laterally, continuous to the genal angles. Hypostome shield-shaped, unilobed, with no denticles posteriorly. Surface of the cephalon is very finely granulated or smooth.

Thorax has 11 segments. Axial ring narrow; axial furrows shallow; axial nodes absent. Pleural furrow shallow and short; pleural ends rounded. Surface almost smooth.

Pygidium short and wide; posterior margin almost straight, anterior margin angular. Furrows, ring and ribs only present anteriorly, posteriorly the pygidium is smooth. Surface almost smooth.

Description

Small trilobites with sagittal cephalic lengths ranging from 2.2mm to 7.0mm, the largest complete specimen found having a total length of 22.2mm (its cephalic length being 6.2mm). The smallest specimen with sagittal cephalic length 2.2mm, a complete specimen, shows the full 11 thoracic segments, thus all specimens are known to be holaspids.

The outline of the complete animal is slightly tapered backward. The trilobed feature is clearly exhibited except at the posterior end of the pygidium where the axial region and the pleural regions are fused together. The thorax is longer than the cephalon and the animal is micropygous.

In plan view (see text-fig. 2.6a, p.80), the cephalic outline less the posterior margin approximates to a semicircle with the anterior margin smoothly curved forward. The maximum breadth is slightly forward of the base of the cephalon due to the shifting forward of the genal angle. The genal angles are smoothly rounded and form parabolic curves or are slightly angular. The posterior margin is approximately straight. Due to deformation the cephalic outline is sometimes longer or shorter than semicircular with the genal angles extended backward and the posterior margin curving forward. In front view (see text-figure 2.6b, p.80), the glabella and the genae are convex, the convexity of the former being slightly stronger than that of the latter. The genae slope steeply and continuously to the lateral cephalic margins, showing slight depressions as they pass the lateral border furrows. In side view (see text-figure 2.6c, p.80), the anterior glabellar margin is thick and overhanging, fused with the anterior border furrow. The glabella reaches the highest point slightly in front of the rear end of its frontal lobe. From there it slopes steadily forward to the anterior margin while toward the rear end it slopes more steeply to the low preoccipital ring. The occipital ring is obtrusive.

The glabella is small, inflated and strongly expanding forward. The glabellar angle ranges from 55° to 80° (mean of 60°) at its entrant angle but forward of this, its posterolateral margins bend outward, gradually widening the glabellar angle to 70° to 80°, although due to compression the angle sometimes reaches 100°. The lateral glabellar corners are smoothly rounded and quite strongly curved, but compression sometimes makes them angular or slightly

The anterior glabellar margin is short and gently and smoothly curves forward. There are no S2 and S3 glabellar furrows. The S1 preoccipital glabellar furrow is narrow and shallow, interrupted medially, while the lateral parts of it form a straight line discontinuous medially. On the internal mould, as in most cases, this furrow is poorly distinguished. The lateral preoccipital pits are circular on the internal mould, transversely elongated on the carapace. The preoccipital ring is shorter (sagittaly) on the carapace than it is on the internal mould. It is low and unobtrusive medially, ridged laterally. The occipital furrow is narrow and shallow curving weakly forward and interrupted medially. The lateral occipital pits are transversely elongated. On the internal mould the occipital furrow is poorly distinguished while the lateral occipital pits are rounded in outline. The occipital ring is obtrusive longer sagittally than the preoccipital ring. The occipital and preoccipital rings are comparatively wide, their width being approximately one third of the maximum cephalic width.

The axial furrows are wide, deep only anteriorly, shallowing gradually rearward, very shallow and indistinct between the preoccipital ring and the genae. The genae are inflated, wide with almost equilateral triangular shapes and sloping almost continuously to the lateral cephalic margin, except for a slight depression interrupting the slopes as they pass the lateral border furrows. The lateral border furrows are very shallow and narrow anteriorly, shallower and indistinct posteriorly especially at the genal angle. The posterior border furrows are distinct adaxially, shallower and indistinct abaxially. The posterior borders are separated only by a low depression from the occipital ring adaxially. They are narrow and swollen adaxially, wider and flatter abaxially toward the genal angles. The lateral borders are widest slightly in front of the genal angles or at the genal angles themselves, narrowing gradually forward. There are no eyes, no facial sutures and no librigenae.

The anterior border furrow is indistinct. The anterior border is wide and flat laterally, narrow and fused together with the anterior glabellar margin and the anterior doublure medially. The anterior doublure is short. The vincular furrow is wide and deep medially, narrowing and shallowing laterally and continuous along the lateral cephalic margin to the genal angle where it terminates.

The surface of the cephalon is very finely granulated or smooth. The hemispherical granules have a diameter much less than 0.05mm and are distributed randomly all over the cephalon.

The hypostome (text-figure 2.6e, p.80) is small, shield-shaped and weakly inflated. Its sagittal length is slightly shorter than its maximum width. The anterior margin is a smooth, forward curve which is continuous on to the anterior wing. The anterior wings have angular distal ends and straight posterolateral margins. The lateral margins taper only slightly backward. The posterior margin is smoothly curved, so that the posterior half of the hypostome has an almost semielliptical shape. The hypostome is unilobed with the median lobe sloping continuously to the margins in all directions except toward the anterior wings where the slopes are reduced as they approach these wings. There are no border furrows. The surface is smooth.

The thorax is similar to those of other phacopids except that it is poorly ornamented or smooth, like most of the species of Dianops.

The pygidium (text-figure 2d, p.80) is very short, wide and transversely vaulted. The anterior margin is angular while the posterior margin is very weakly curved rearwardly. The axial ring is inflated anteriorly, tapering backward and fused with the pleural and border regions posteriorly. The maximum number of rings observed is 3 although the third ring is usually missing. The rings are weakly swollen and are separated by a narrow and shallow ring furrows from one another. The terminal piece is smooth. The axial furrows are wide and shallow anteriorly, fading away posteriorly. The pleural region bears 2 pairs of pleural furrows which mark the presence of 2 pairs of pleural ribs. The pleural furrows are shallow and narrow. The interpleural furrow and border furrow are absent. The border is indistinct. Generally all the furrows tend to diminish posteriorly.

The surface of the pygidium is almost smooth.

Comparison and discussion

The most significant characteristic of this species is that it is very small compared to other species of *Dianops*. Although the size frequency distribution (see text-figure 2.7, p.80f) indicates that the whole population has been sampled, the largest individual of this species is still very small compared to the size range observable in other species of *Dianops* studied. The smallest holaspids of this species (no meraspids found in this species) is also smaller than the late meraspids of other *Dianops* species studied, except *D. limbatus* where meraspids were not found.

Apart from this fact, *D. combensis* sp. nov. can be differentiated from other species of *Dianops* by its very wide cephalon, frontal glabellar lobe and occipital and preoccipital rings. The maximum cephalic width of this species is about twice its sagittal length, the maximum breadth of its frontal glabellar lobe usually larger than its sagittal length, while the widths of its preoccipital and occipital rings are about one third of its maximum cephalic width. Furthermore it also has in comparison to other species of *Dianops*, a very poorly developed preoccipital ring, very wide axial furrows which are very shallow and indistinct posteriorly and a very shallow border furrow around the genal angle. Furthermore *D. combensis* has a deeper vincular furrow and a short but wider pygidium, when compared to other species of *Dianops* (the pygidial length is shorter than half the maximum pygidial width of this species). The closest species are *D. vicarius* Chlupac 1961 and *D. typhlops* (Gurich 1896). Both of these species occupy an earlier stage compared to *D. combensis* and also their occurrences are restricted to Eastern Europe (*D. vicarius* has so far only been found in Czechoslovakia, occupying Zone IV of the Famennian, while *D. typhlops* is restricted to Poland and Zone ?IV/V of the Famennian).

D. vicarius resembles *D. combensis* in having a small glabella which slopes steadily forward, wide occipital and preoccipital rings, very faint lateral border furrows and a very weakly granulated surface of the cephalon. However in comparison to *D. combensis*, *D. vicarius* has a narrower cephalon and glabella with a narrower glabellar angle. The preoccipital ring of *D. vicarius* is higher than that of *D. combensis* although the median part of the preoccipital ring is not lobed in both species. The axial furrows of *D. vicarius* are narrower but distinct both posteriorly and anteriorly where, as in *D. combensis* even though they are wider and deeper anteriorly, they become shallower and indistinct posteriorly. The S2 and S3 glabellar furrows and the facial suture which are present in *D. vicarius* are absent in *D. combensis*. The vincular furrow of *D. combensis* is deeper than that of *D. vicarius*. Furthermore the pygidium of *D. vicarius* is longer and narrower than that of *D. combensis*.

D. typhlops resembles *D. combensis* in having a small glabella, a narrow glabellar angle, a low preoccipital ring, wide axial furrows, a deep vincular furrow and a very weakly granulated surface to the cephalon. In terms of differences, *D. typhlops* has a slightly narrower cephalon and glabella, more distinct axial furrows posteriorly, distinct border furrows and a more swollen lateral border compared to *D. combensis*. The facial suture is present in *D. typhlops* but absent in

D. combensis. The pygidium of *D. typhlops* is longer, narrower and has clearer furrows than that of *D. combensis*.

Using its unique characteristics, as discussed earlier in this topic (p. 86), *D. combensis* can be easily distinguished from all other species of *Dianops*. Thus the unique characteristics of *D. combensis*, with respect to all other species of *Dianops*, justifies its specific status.

Comment on Waters' specimens.

All the present author's collection of *D. combensis* come from the Combe fossil band which is given the status of type locality for this species. However in 1971 Waters collected some specimens which the present author can classify as belonging to *D. combensis*, despite some morphological variations between them and the type specimens. These specimens come from localities 1D and 4.

The present author has some doubt on the validity of the first occurrences (i.e. the specimens from locality 1D). These specimens occur in 3 slabs of slate which are very different from other slate found in the same locality. These *D. combensis* slates are more consistent with slates typical of the areas West and North of Ramshorn Down where the type locality of this species is sited. The slates are poorly cleaved and yellow and greenish in colour contrasted from the slates of the Lounston fossil band which are bluish-grey in colour and have a better cleavage.

The second occurrence (i.e. the specimens from locality 4) created a small problem on the stratigraphical range of this species. The stratigraphical range for this locality as diagnosed by the presence of *M. dichotoma*, can range from lower Zone V to upper Zone VI of the Famennian, but according to Gooday (1978) the form of *M. dichotoma* here (in locality 4 and elsewhere in the Rora Slate) is typical of Zone VI of the Famennian. The position of this locality which is very close to the contact between the Rora Slate and the Mt. Ararat Chert suggests that it belongs to the uppermost part of Zone VI of the Famennian, probably not very far from the range of ages given to the type locality of this species.

2.4.5 *Dianops* Sp. A

(Plate 3, figure 13)

Localities: Localities 1B, 1D and 5 (see text-fig. 1.2a & b, p.5f).

Horizons: The Rora Slate: Localities 1B and 1D - *sphaeroides* subzone (≡ Zone VIβ of the Famennian) diagnosed by the presence of *Epiwocklumeria*.
Locality 5 - *paradoxa* Zone (≡ Zone VIβ of the Famennian) diagnosed by the presence of *Parawocklumeria*.

Materials: Specimen no. AD 1862 (WC) from locality 1D
Specimen no. Zo 4679 (LC) from locality 1B
Specimen no. AD 1981 (WC) from locality 5

Remarks

The cephalon is long with its sagittal cephalic length only a little less than the maximum cephalic width. The anterior cephalic margin is angular. The glabella is longer than its maximum width. It is quite inflated. The posterolateral glabellar margins are strongly bent outward, the lateral glabellar corners truncated. The S1 preoccipital glabellar furrow and the occipital furrow are interrupted medially, the former is straight while the latter is forwardly curved. The lateral occipital and preoccipital pits are transversely elongated. The preoccipital ring is low and not lobed medially, but is ridged laterally. The occipital ring is obtrusive, short and narrow. The axial furrows are narrow and shallow and continuous posteriorly. The genae are weakly inflated, sloping steadily towards the lateral cephalic margin. The border furrows are indistinct. The surface of the cephalon is smooth.

The closest to this species is *D. griffithides griffithides*, where both of them have shallow, narrow and strongly bent axial furrows, indistinct border furrows and very poorly developed preoccipital rings. However this species differs from *D. griffithides griffithides* in having a markedly longer cephalon and glabella compared to its width, a very short occipital and preoccipital ring and a smooth cephalic surface.

2.4.6 *Dianops* sp. indet. (pygidia)

Localities: Localities 1A, 1C and 1D of the Lounston fossil band (see text-fig. 1.2b, p.5f).

Horizons: The Rora Slate - *sphaeroides* subzone (≡ Zone VIβ of the upper Famennian) diagnosed by the presence of *Epiwocklumeria*.

Materials: Specimens nos. Zo 4647-4648 (LC) from locality 1A, Zo 4675-4676 (LC) from locality 1C and AD 1858/9 and AD 1872 (WC) from locality 1D.

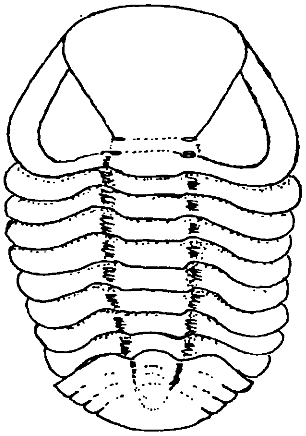
Remarks

The pygidium is small; short and wide with its maximum breadth being longer than twice its sagittal length. The posterior margin of the pygidium is very weakly curved rearward while the anterior margin is angular at the pleural region and strongly curved forward at the axial region. The pygidium is almost totally smooth except for the anterior part where the ring and ribs are distinguishable. The pygidium bears 1 or 2 axial rings and 1 or 2 pairs of pleural ribs which are marked by the number of ring furrows for the former and the number of pairs of the pleural furrows for the latter. The axial furrows are only distinguishable anteriorly. Posteriorly the axial and pleural regions are fused together. The interpleural furrow andthe border furrow are absent. The surface of the pygidium is smooth or very weakly granulated.

2.4.7 Dianops sp. indet. (juvenile)

(Text-figure 2.8 , below)

Locality:	Locality 1C of the Lounston fossil band (see text-fig. 1.2b, p. 5f).
Horizon:	The Rora Slate - sphaeroides subzone (≡ Zone VI β of the Famennian) diagnosed by the presence of Epiwocklumeria.
Materials:	Specimen no. Zo 4672 a,b.



Text-figure 2.8 :

The reconstruction of Dianops sp. indet.

(10 X)

Remarks

A very small trilobite with its sagittal cephalic length about 2.3mm (maximum width = 4mm). The cephalon is broken but the remaining gena is smooth (no eye) and bears genal spines. The glabellar angle is about 55°. The surface of the remaining part of the cephalon is smooth.

The specimen bears 8 thoracic segments, each of which is short (sagittaly) and quite long (transversely). The surface of the thorax is smooth.

This specimen also bears a broken transitory pygidium which is very small, short and narrow. The interpleural furrows are well marked at the pygidial margin and weakly marked adaxially. 3 pleural ribs are present anteriorly (marked by the number of interpleural furrows) while posteriorly the pleural region is smooth. The axial region is broken. The surface of the pygidium is smooth.

The absence of the eye and the smooth surface suggest that this specimen belongs to the genus Dianops. Furthermore the transitory pygidium of this species differs from those of the juveniles of Phacops or Cryphops in having a weakly marked interpleural furrow adaxially and a smooth pleural region posteriorly. In the juveniles of Phacops and Cryphops interpleural furrows are well marked from the ring to the pygidial margin and no smooth pleural regions are formed posteriorly.

These smooth pleural regions might represent a true pygidium which is similar to the adult's pygidium. Since this is the first time that the juvenile pygidium of Dianops is reported, it cannot be compared against its own genus.

Thus this juvenile is referable to Dianops and clearly distinct from those of the juveniles of Phacops and Cryphops.

2.5 Remarks on ontogeny

In the Lounston fossil band juvenile phacopids occur quite frequently. Elsewhere juveniles were not found. Most of the juveniles probably belong to the late meraspid stage although the exact stage cannot be certain due to lack of complete specimens. The juvenility of the species is interpreted mainly by the presence of the genal spines on the cephalon and the characters of the pleural tergites on the pygidium. The relative size only cannot be used since the smallest observed holaspids in *D. combensis* appeared to be much smaller in size compared to the juvenile of other species. The juveniles also differ from the adult forms in a small number of regularly occurring characteristics, although the mode of change of these from meraspis to holaspis differs from genus to genus. These features are as follows:

1. Cephalic outline

The sagittal cephalic length/maximum cephalic width ratio (A:I) in the juveniles of the genera *Phacops* and *Cryphops* is smaller than in the adult form, while this ratio in the juveniles of genus *Dianops* is bigger than in its adult form. The posterior margin of all phacopids seems to be straighter in juveniles than in adults.

2. Glabella

In all genera the glabella of the juvenile is more inflated than that of the adult. The glabellar angle of the juveniles in *Phacops* and *Cryphops* is wider than in their adults, but in *Dianops* the glabellar angle of the juvenile is narrower than that of the adult.

3. Genae

Like the glabella the genae of all genera are more inflated in the juvenile than it is in the adult. Within the meraspids (all genera) the genal spine is longer in smaller individuals and shorter in the larger ones. Juvenile librigenae in all genera are usually missing due to a functional facial suture. The functional facial suture was inherited by the adult of *D. tripartitus* and *Cr*? *wocklumeriae lounstonensis* but not in any species of *Phacops*.

4. *Ornamentation*

Juveniles of *Phacops* and *Cryphops* usually bear a heavier granulation than the adults, but in *Dianops* the juvenile appears to have a smoother surface of cephalon than its adult has.

5. *Pygidium*

The transitory pygidium in the juvenile of all genera are longer and narrower than the pygidium of the adult. The interpleural furrows are present in the juvenile but absent in some adults (including all the pygidia found so far from the study area) the border region is absent in the juvenile while it is present in the adult.

The interpleural furrows of the transitory pygidium of *Phacops* and *Cryphops* are well marked throughout the whole pleural region while in *Dianops* the interpleural furrows are only well marked at the margin and fade away adaxially.

CHAPTER 3

STRATIGRAPHY

3.1 Introduction

Elucidation of the taxonomic and geographical relationships of the trilobite faunas of the Lounston area in comparison with those elsewhere in SW England and Europe requires that their stratigraphical position be fixed with some accuracy, and the substance of this chapter deals with this problem. In doing so, all the established biostratigraphic zonation schemes were studied and applied to the study area. However since only the uppermost part of the Famennian (do V - do VI) and the lowermost Carboniferous have a bearing on the age of the Rora Slate (Selwood 1977), only the pertinent parts of the zonal schemes will be discussed.

3.2 The stratigraphy of the Upper Devonian

The Upper Devonian marine rocks of South Devonshire, like those elsewhere are mainly correlated by means of ammonoid, ostracod or conodont biostratigraphy. Recently a trilobite biostratigraphy was introduced by Alberti (1979) and Maksimova (1980), for use in the correlation of the marine Upper Devonian of the Old World Province (excluding the Tasman, New Zealand and Cordilleran subprovinces). Below are brief summaries of these biostratigraphic correlations with special reference to the Upper Famennian (see also Table 3.1, p. 95f).

*Note: The term "do" (≡ Oberdevon ≡ Upper Devonian) was used in place of "to" which was also used in the same context (for details see Zeigler (1971).

⟶
Text-figure 3.1

Table 3.1 : Ammonoid, ostracod, and trilobite biostratigraphy of the Upper Devonian and the stratigraphic positions of the studied localities.

SERIES	STAGES	STUFEN		AMMONOID ZONES		OSTRACOD ZONES	TRILOBITE ZONES		POSITION OF THE STUDIED LOCALITIES
LOWER CARBONIFEROUS									Mt.Ararat Chert
UPPER DEVONIAN	FAMENNIAN	WOCKLUMERIA	do VIβ	Prionoceras spp.- Cymaclymenia euryomphala		interregnum	Phacops wedekindi —	Phacops(Om.) accipitrinus	RORA SLATE **Combe** F.B. Lounston F.B.
				Parawocklumeria paradoxa	Wocklumeria sphaeroides Kamptoclymenia endogona	Maternella hemispherica —			
			do VIα	Kalloclymenia subarmata		M. dichotoma	Dianops griffithides		
		CLYMENIA	do Vβ	Gonioclymenia speciosa					
			do Vα	G. hoevelensis					
		PLATYCLYMENIA	do IV	Platyclymenia annulata		Richterina (? F.) intercostata	———		
			do IIIβ	Prolobites delphinus					
			do IIIα	Pseudoclymenia sandbergeri		interregnum			
		CHEILOC.	do IIβ	Sporadoceras pompeckji		Entomozoa(Richteria) serratostriata—	Trimerocephalus mastophthalmus —		
			do IIα	Cheiloceras curvispina		E.(N.) nehdensis	Ductina ductifrons		
	FRASNIAN	MANTICOCERAS	do Iδ	Crickites holzapfeli		Entomoprimitia(E.) variostriata (7 Zones + 2 interreg.)	———		
			Iγ	Manticoceras cordatum		Ber .(Ra.) cicatricosa			
			Iβ			interregnum			
			Iα	Pharciceras lunulicostata					
MIDDLE DEVONIAN									

3.2.1 The ammonoid biostratigraphy

Ammonoid biostratigraphy is regularly used in the chronostratigraphical correlation of the marine Upper Devonian because of the widespread distribution and short zonal intervals of these fossils. Major works on establishing the ammonoid chronological scale were carried out mostly in the Rhenish Schiefergebirge (Germany) and these works are fully summarized by House (1979). The zonal division of the Upper Devonian based on ammonoids can be seen in Table 3.1, p. 95f. The clymenids play a very important role in the Upper Famennian zonation and appear at the beginning of the *Platyclymenia* *Stufe* (do III) achieving their highest diversity in the *Clymenia* *Stufe* (do V) and the *Wocklumeria* *Stufe* (do VI) and becoming extinct shortly before the Carboniferous. Only the genus *Cymaclymenia* managed to survive until the end of the Devonian.

The Clymenia Stufe

This *Stufe* is divided into 2 zones, the *Gonioclymenia* *hoevelensis* Zone (do Vα) and *G.* *speciosa* Zone (do Vβ), marked by the presence of *G.* *hoevelensis* and *G.* *speciosa* respectively. This *Stufe* also shows the diversification of the clymenids with complex sutures including the introduction of the genera *Kosmoclymenia*, *Cymaclymenia*, *Gonioclymenia* and *Sellaclymenia* as well as continuing the simple suture stocks like *Clymenia* itself.

The Wocklumeria Stufe

This *Stufe* is divided into 3 zones; the *Kalloclymenia* *subarmata* Zone (do VI α), the *Parawocklumeria* *paradoxa* Zone (lower to middle do VI β) and the *Prionoceras* spp - *Cymaclymenia* *euryomphala* Zone (uppermost of do VIβ). The *subarmata* Zone marks the entry of the genus *Kalloclymenia* in Germany, although this genus might have appeared earlier in some other places (Selwood 1960). A little higher within this zone appear the distinctive genera *Trochoclymenia*(?), *Sphenoclymenia*, *Soliclymenia*(?) and new species of more conservative genera derived from the Zone below.

The *paradoxa* Zone marked the entry of the genera *Parawocklumeria*, *Triaclymenia*, *Kamptoclymenia*, *Postglatziella* and new species of older genera. This zone can be divided into 2 subzones; the *Kamptoclymenia endogona* subzone (lower part of the *paradoxa* zone) and the *Wocklumeria sphaeroides* subzone (upper part of the *paradoxa* zone) which mark the entry of the genera *Wocklumeria* and *Epiwocklumeria*. No clymenids except *Cymaclymenia* range above the top of the *paradoxa* zone.

In the *Prionoceras* spp—*C. euryomphala* zone only *cymaclymenia* survived, together with the prionoceratids, the latter continuing to the *Gattendorfia Stufe* of Lower Carboniferous while *Cymaclymenia* marked the end of the Devonian. The prionoceratids began a new ammonoid fauna when they reached the Carboniferous.

3.2.2 The ostracod biostratigraphy (see table 3.1, p.95f).

The ammonoids appear to be rare in some places, particularly in deep water where the ostracods take their place in the chronostratigraphic correlation. However the value of the ostracod biostratigraphy in the Upper Famennian is not as great as that of the ammonoids. The whole Upper Famennian (except the uppermost part) falls into only one zone, that is the *Maternella hemispherica* - *M. dichotoma* Zone (lower do V to middle do VI β), marked by the occurrence of *M. hemispherica* and/or *M. dichotoma*. The uppermost part of the Devonian was marked by the zone of interregnum between the *Maternella* suite and the

Carboniferous ostracods. The beginning of this interregnum is still obscure but evidence from the present study suggests that it began later than the beginning of the *euryomphala* Zone of the clymenids (see Table 3.1 , p.95f).

Some efforts have been made by Gooday (1978) to divide this long ranging *hemispherica* - *dichotoma* Zone into lower and upper parts. A new rounded form of *M. dichotoma* in the Rora Slate was established by him as the marker of the upper part of this zone. However this form has only been reported from the Rora Slate and all the *M. dichotoma* in the present author's collections and Waters' collection have this form. But since the base of the Rora Slate cannot be found, the present author expresses his doubt about the use of this form as a subzone index. This special form might be just a local variation of the species.

Before this new form can be accepted for use as stratigraphic markers, a complete succession must be produced, although this seems to be impossible in the structurally very complex area in which the Rora Slate is situated.

3.2.3 The conodont biostratigraphy (see Table 3.1, p.95f)

No conodont index fossils have been found in the Rora Slate.

3.2.4 The trilobite biostratigraphy (see Table 3.1, p.95f)

Like the ostracods the trilobite zones also have very long ranges in the upper Famennian. The whole upper Famennian corresponds to the *Phacops wedekindi* - *Dianops griffithides* Zone (lower do Vα to upper do VIβ), *Ph. wedekindi* and *D. griffithides* extending throughout the whole zone. This zone also marks the occurrences of *Cr? ensae*

Cr? wocklumeriae, *D. limbatus*, some *Typhloproetus*, *Drevermannia*, *Chaunoproetus* and *Cyrtosymbole*. The upper part of this zone was named as the *Phacops* (*Omegops*) *accipitrinus* subzone which marked the occurrences of the subgenus *Phacops* (*Omegops*). The *accipitrinus* subzone is equivalent to the whole range of the *Wocklumeria* *Stufe* (do VI). However Selwood (1960) found this subgenus in the lower *Stufe*, that is, the *Clymenia* *Stufe* (do V). The end of the *wedekindi-griffithides* marked the upper limit of all the phacopid trilobites and some proetids.

All these biostratigraphic zonation schemes were used in determining the age of localities studied.

3.3 The Liverton-Bickington-Ilsington succession (column 4, text-fig.3.1A, p.99f).

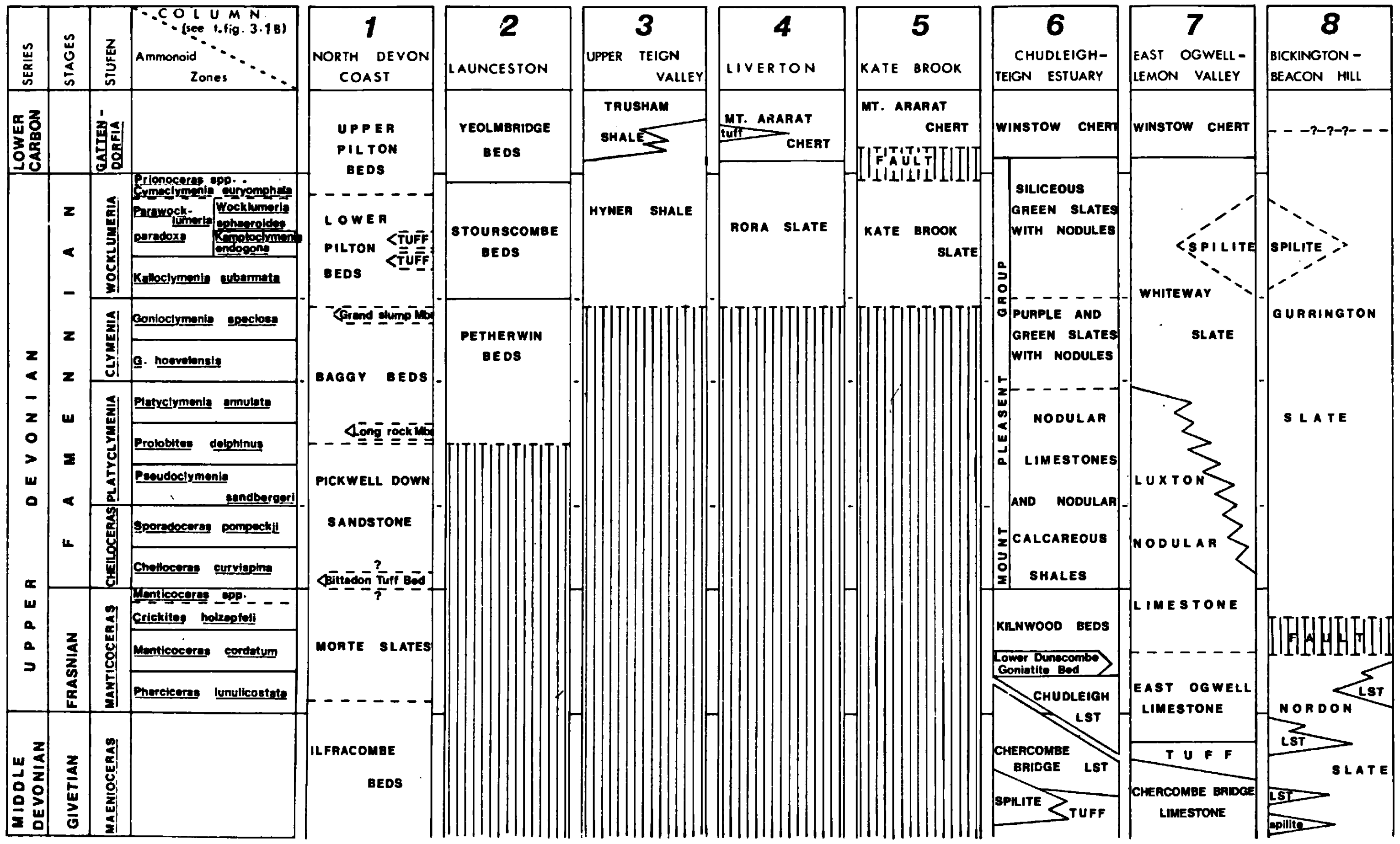
The Liverton-Bickington-Ilsington succession in which the rocks of the study area are situated is bounded on the North by the Silverbrook Fault and on the South by the Holne Thrust. The oldest formation in this succession is the Rora Slate.

The name Rora Slate is used for a formation consisting of grey green and dark purple slates with rare thin limestone layers and layers of slate with calcareous and siliceous nodules. A rich trilobite-clymenid ostracod fauna is developed in a number of localities including Lounston, Combe (etc.). According to Selwood in House *et al* (1977) most of this formation belongs to the *Wocklumeria* *Stufe*; The lower horizons are not older than the upper part of the *Clymenia* *Stufe* while the top horizons may range into the *Gattendorfia* *Stufe*. At least 150m of slates being recorded by the I. G. S. --- (see Sheet 339 (1976)). The base of the Rora Slate is not exposed while

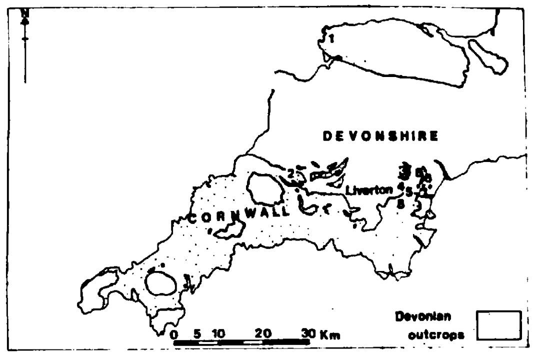
⟶
text-figure 3.1

TEXT-FIGURE 3.1

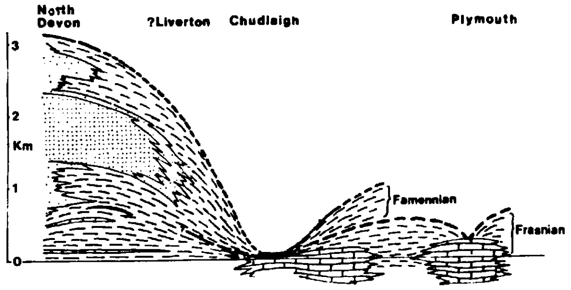
A. STRATIGRAPHIC COLUMNS FOR SOME OF THE SW-ENGLAND UPPER DEVONIAN SUCCESSION [after Austin et. al 1969, Goldring 1962,1969, Goldring et.al. 1967, House & Selwood 1965, House et. al. 1977]



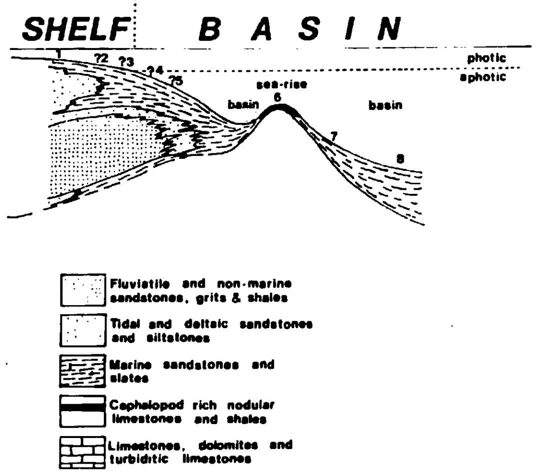
B. Devonian outcrop in SW-England and the location of the successions in text-figure 3.1 A



C. Upper Devonian section from N. Devon to Plymouth (after House 1975[I] and House et.al. 1977)



D. Famennian bathymetry (modified from House 1975[II] Paproth & Streel 1970) with above localities positioned according to their fossil content and lithology



its top is overlain by the Mt. Ararat Chert of the Lower Carboniferous. The stratigraphical positions of the Rora Slate and of the fossiliferous localities studied for this thesis are discussed below.

3.4 The Lounston fossil band (locality 1)(see text-fig. 1.2b, p.5f)

For detail on the faunal lists of this fossil band see table 3.2, p. 100f.

3.4.1 Stratigraphical details based on the clymenids

The base of this fossil band (locality 1A) as indicated by the presence of the genus *Epiwocklumeria*, has an age within the *sphaeroides* subzone (upper *paradoxa* Zone). Also found are some other distinctive genera including ?*Parawocklumeria*, ?*Postglatziella* and *Kosmoclymenia*. These distinctive genera are absent in all other localities (1B and 1C). Locality 1B yields a very great number of clymenids but all these clymenids are of common genera except for a very rare occurrence of the genus *Kenseyoceras* which marks the *paradoxa* Zone (including the *sphaeroides* zubzone). Locality 1C which is the uppermost fossiliferous locality studied in this fossil band, yields only the genera *Cymaclymenia* and *Kosmoclymenia*. The presence of the latter genus indicates that the top of the Lounston fossil band is still below the upper limits of the *paradoxa* Zone.

3.4.2 Stratigraphical details based on the ostracods

The presence of *M. hemispherica* and *M. dichotoma* at the bottom and the top of this fossil band indicates that this fossil band is in the range of the *hemispherica* - *dichotoma* Zone ($\equiv$ lower do V α to upper do VI β). *M. hemispherica* is very rare at the bottom of this fossil band (locality 1A) absent at both sublocalities 1B and 1D and quite rich at the top of the fossil band (locality 1C). In contrast,

→ Table 3.2

TABLE 3.2 Faunal lists of the Rora Slates , their corresponding ages and localities

Age	UPPER DEVONIAN							L.CARB.	
Series	FAMENNIAN								
Lists of species — Stufen	PLATYCLYMENIA			CLYMENIA		WOCKLUMERIA		GATTEN.	Localities
Zone	III α	III β	IV	V α	V β	VI α	VI β		(see map in text-figure 1.2
Ph. granulatus (Münster, 1840)	x	x	x	X	X	X	X		1A, 1D, 1C? and 3
Ph. wedekindi microps n.ssp.				X	X	X	X		1A, 1D and 5
Ph. wedekindi occidentalis n. ssp.							XX		1A and 1D
Ph. wedekindi ssp.A							XX		1A
Ph. sp. indet.									1A, 1B, 1C, 1D, 3 and 5
Ph.(Omegops) sp. B						X	X		9
Cr.? wocklumeriae lounstonensis n. ssp.							XX		1A
Cr.? *ensae* R.& E.Richter, 1926				X	X	X	X		1D
Cr. sp. A							XX		1D
D. limbatus(Reinh. Richter, 1848)				X	X	X	X		1A, 1C and 10
D. griffithides griffithides (R.& E.Richter, 1919)				X	X	X	X		1A, 1B, 1C and 1D
D. tripartitus (Thomas, 1909)				x	x	x	XX x		1A, 1C and 1D
D. combensis n. sp.							x XX		1D?, 2 and 4
D. sp. A							x XX		1B, 1D and 5
D. sp. indet.									1A, 1C, 1D, 7,8,11 and 12
T. subcarintiacus Rud. Richter, 1913				X	X	X	X		1A, 1D, 6?
T. ?*microdiscus* Rud. Richter, 1913				X	X	x	x		1A
Ch. palensis (Rud. Richter, 1913)	X	X		X	X	X	X		1A, 13
Ch. tietzei(R.& E. Richter, 1919)				X	X	X	X		1A
Dr. schmidti Rud. Richter, 1913				X	X	x	x		1A
?*Archegonus* sp.							XX		2
proetids sp. indet.									1A, 1C, 6
Epiwocklumeria sp.							XX		1A
?*Parawocklumeria* sp.							XXXX		1A and 5
?*Postglatziella* sp.							XXXX		1A
?*Kalloclymenia* sp.						X	X		1A
Kenseyoceras sp.							XXXX		1B
Cyrtoclymenia sp.				X	X	X	X		1A and 1B
Kosmoclymenia sp.				X	X	X	X		1A, 1B, 1C and 9
Cymaclymenia sp.				X	X	X	X		1A, 1B, 1C, 1D, 2 and 3
M. hemispherica (Reinh. Richter, 1848)				X	X	X	X x		1A, 1C and
M. dichotoma (Paeckelmann, 1913)				X	X	X	X x		1A,1B,1C,1D,3,4,6 and13
R.(R.) striatula (Reinh. Richter, 1848)	X	X	X	X	X	X	X		1A,1B,1C,1D,2,3,4,5,6,7, 11,12 and 13
R.(R.) costata (Reinh. Richter, 1869)	X	X	X	X	X	X	X		1A,1B,1C,1D,2?,4,5 and 6
R.(F.) semen (Jones, 1895)	X	X	X	x	x	x	x		2
?R.(?F.) intercostata (Matern, 1929)	X	X	X				?xx		1A and 1D
? conodonts									1A and 1C
spiriferids sp.									1A, 1B, 1D, 6? and 7?
orthids sp.									1A, 1C, 1D, 2 and 5
lingulids sp.									4
Petraia sp.									1A,1B,1C,1D,2,12 and 13
?*Petraia* sp.									12
Fenestella sp.									1B
bivalves (*Posidonia* sp. etc.)									1A,1B,1C,1D,5,6,7,12&13
crinoids									1A,1B,1C,1D,2,6,7,and 12

M. dichotoma is comparatively rich at the bottom, rarer towards the top (very rare at the top). The latter species is present at all localities. Other ostracods accompanying these two index fossils are *Richterina* (*R.*) *striatala* which is very rich at all sublocalities, *R.* (*R.*) *costata* which is richer at the bottom, less rich towards the top and ?*R.* (?*F.*) *intercostata* which is rarely present at localities 1A and 1D. The latter species according to many authors, was extinct before the *Clymenia Stufe* (do V), and its presence marks the lower zone i.e. *intercostata* Zone (do III to do IV). However this species, in addition to the absence of its muscle pits, also shows narrower ribs compared to that of *R.* (*F.*) *intercostata* elsewhere.

3.4.3 Stratigraphical details based on the trilobites

The occurrence of *D. griffithides griffithides* at all sublocalities and *Ph. wedekindi sensu lato* at localities 1A, 1D and 1C indicates that the Lounston fossil band is in the range of *wedekindi* - *griffithides* Zone (≡ lower do V α to upper do VIβ). *Cr. ensae*, *D. tripartitus*, *D. limbatus* and *Ph. granulatus* also agree with the above zonation. *Cr? ensae* is only found at locality 1D whereas *D. tripartitus* and *Ph. granulatus* can be found at localities 1A, 1D and 1C, while *D. limbatus* is only found at sublocalities 1A and 1C. In general, phacopids with eyes are more abundant at the lower horizon than at the top of this fossil band. In contrast, the blind phacopids are richer at the top horizon than the bottom of this fossil band.

3.4.4 The age of the Lounston fossil band

As a conclusion, based mainly on the clymenids, with some support from the ostracods and trilobites, this fossil band must have an age within the range of the *sphaeroides* subzone (≡ middle do VIβ) of the *paradoxa* Zone (≡ lower to middle do VIβ). The local zonation offers a guide, yet to be proved, that this fossil band might lie at the top of the *sphaeroides* subzone.

3.5 The Combe fossil band

This fossil band provided a very poor fauna with some specialized species. From nearly 200 specimens studied only 10 species were found and among them *Dianops combensis* n.sp. dominates the others with more than 130 occurrences. It is also the only phacopid trilobite here. The other species are very rare. Among those which are important stratigraphically are *Cymaclymenia euryomphala* which represents the only ammonoid here; *Maternella hemispherica* n.ssp? *Richterina* (*R.*) *striatula*, *R.* (*F.*) *semen* and *Archegonus* sp. (1 cephalon and 2 pygidia). Other fossils include *Chonetes* sp., *Petraia* sp. bivalves (1 species) and crinoid ossicles.

The absence of other clymenids except *Cymaclymenia euryomphala* suggests that this fossil band belongs to the *euryomphala* Zone (≡ upper do VIβ) of the Famennian. The presence of *M. hemispherica* n.ssp? which indicates the *hemispherica* - *dichotoma* Zone (do V to VI), suggests that this zone overlaps the *euryomphala* Zone of the clymenids. The zone of interregnum between the *Maternella* suite and the Carboniferous ostracods might start a little later than the *euryomphala* Zone of the clymenids. Surprisingly, *R.* (*F.*) *semen* (confirmed by Gooday), which is thought to be extinct together with the *R.* (?*F.*) *intercostata* at this level is still present here. This is the second occasion that this species *R.* (*F.*) *semen* has been found in the upper part of the *hemispherica* - *dichotoma* Zone, the first time being Gooday's (1978) discovery which is also from the

Rora Slate. The trilobites do not include any index species.

The overlap between the clymenid *euryomphala* Zone and the ostracod *hemispherica* - *dichotoma* Zone suggests that this fossil band has an age somewhere in the lower part of the *euryomphala* Zone.

3.6 Other fossiliferous localities in the Rora Slate

With very few details available, a precise age for the other localities cannot be expected, although some of these localities have produced fossils which enable a more precise stratigraphical positioning to be made. Brief summaries of the age of all the fossiliferous localities and their index fossils are shown in the table below.

Locality	Chronological Zone (range)	Index fossils
1	do VI	*Epiwocklumeria ?applanata* (Wedekind, 1908)
2	do VI	*Cymaclymenia euryomphala* (Schindewolf, 1926)
3	do V-V ?(do VI)	*Maternella dichotoma* (Paeckelmann, 1913)
4	do V-V ?(do VI)	*Maternella dichotoma* (Paeckelmann, 1913)
5	do VI	?*Parawocklumeria* sp. indet.
6	do V-VI ?(do VI)	*Maternella dichotoma* (Paeckelmann, 1913)
7	do IV-VI	*Dianops* sp. indet.
8	do IV-VI	*Dianops* sp. indet.
9	do VI	*Phacops* (*Omegops*) Sp. B
10	do V-VI	*Dianops ?limbatus* (Reinh. Richter, 1848)
11	do IV-VI	*Dianops* sp. indet.
12	do IV-VI	*Dianops* sp. indet.
13	do V-VI ?(do VI)	*Maternella dichotoma* (Paeckelmann, 1913)

Note: ? (do VI) - Waters 1978 (see p. 97)

Text-figure 3.3 : Stratigraphical positions of the fossiliferous locations in the Rora Slate determined by their fossil compositions.

3.7 The stratigraphical position of the Rora Slate

Among the studied localities there are none which represent either the bottom or the top of the Rora Slate so the age given for each of them does not really reflect the range of age of the entire formation. However the two main localities (loc. 1 and 2) studied are situated very close to the contact between the Rora Slate and the overlying Lower Carboniferous Mt. Ararat Chert (the contact being observed as gradational by Ussher (1913)). Therefore the age presented by these localities should be regarded as close to the upper limit of the age range of the Rora Slate. It means that the upper limit of the Rora Slate must be younger than the euryomphala Zone or within the zone itself. Since this euryomphala Zone is very short elsewhere, Selwood's (1977) presumption that the upper limit of this formation may cross the Devonian/Carboniferous boundary into the Gattendorfia Stufe may be correct. The base of the Rora Slate is not known, but according to Selwood (1977), it has an age equivalent to the upper part of the Clymenia Stufe.

The presence of occasional thin limestone layers, siliceous and calcareous nodules and a quite rich benthic fauna suggests a shallow origin for this formation, probably on the shelf slope far away from shoreline.

3.8 Equivalent Upper Devonian elsewhere in SW England

3.8.1 The Teign Valley succession (Column 3, text-fig. 3.1A, p.99f)(Selwood in House et al 1977)

Toward the North, the Hyner Shale is the closest lateral correlative of the Rora Slate. The Hyner Shale is relatively unfossiliferous compared to the Rora Slate, and its base, like that of the Rora Slate, is unknown. The Hyner Shale probably extended into the Gattendorfia Stufe of the Lower Carboniferous where it was overlain by the Trusham Shale.

3.8.2 The Kate Brook succession (Column 5, text-fig. 3.1A, p. 99f) (Selwood in House et al 1977)

The closest lateral correlative of the Rora Slate toward the south is the Kate Brook Slate. This slate does not provide much detail on the upper Famennian, but the fauna of spiriferids here suggests that the formation is in part at least Late Devonian in age. Fauna and lithology suggest a shelf origin for this formation.

3.8.3 The Bickington-Beacon Hill succession (Column 8, text-fig. 3.1A, p. 99f) (Selwood in House et al 1977)

In this succession which is widely exposed South-West of Newton Abbot, the equivalent Upper Devonian for the Rora Slate is the Gurrington Slate. It is a purple and green slate with rare ferrugneous or siliceous nodules and local development of calcareous grey siltstones and silty slates which appear to represent distal turbidites. The formation is very rarely fossiliferous, its fauna consisting of irregularly distributed pelagic animals dominated by the ostracods and bivalves. The base of this formation, Upper Frasnian in age, is separated from the underlying Middle Frasnian Nordon Slate by a fault. The Gurrington Slate may range up to the Gattendorfia Stufe of the Lower Carboniferous. Fauna and lithology suggest a basinal origin for this formation.

3.8.4 The Chudleigh succession (Column 6, text-fig. 3.1A) (Selwood in House et al 1977)

The whole range of the Upper Devonian and parts of the Givetian are available in this succession. The base of this succession, the

Chudleigh Limestone which is Upper Givetian and Lower Frasnian in age, rests on the Bickington Thrust and is overlain by the Middle Frasnian Kiln Wood Beds. The base of the Kiln Wood Beds is represented by the thin Lower Dunscombe Goniatite Beds. The Kiln Wood Beds, 8.4m thick, carry ammonoids of the *cordatum* Zone and conodonts of the *triangularis* and *gigas* Zones. Overlying this bed is a typical "schwelle" succession, the Mt. Pleasant Group; the lower part of this group consists of nodular limestones and nodular calcarous shales, carrying the *Cheiloceras* and *Platyclymenia Stufen*. The 2 higher units of this group are composed of shales with nodules, often richly fossiliferous. The fossil content of these units show a typical "schwelle" assemblage with ammonoids, trilobites, ostracods, conodonts and some other phyla. The trilobites include *Ph. granulatus*, *Ph.* (*Om.*) *accipitrinus*, *Cr? ensae*, *D.griffithides* and *D. anophthalmus* and no proetids (House & Butcher 1973). The upper unit of the Mt. Pleasant Group carries the *Wocklumeria Stufe*. The total thickness of this group is 40m and at the top this "schwelle" facies is terminated by the appearance of the Lower Carboniferous Winstow Chert.

Most of the Rora Slate is equivalent to the upper unit of the Mt. Pleasant Group.

3.8.5 The East Ogwell-Lemon Valley succession (Column 7, text-fig. 3.1A, p.99f)(Selwood in House *et al* 1977)

The base of this succession being the East Ogwell Limestone of Middle Givetian to late Middle Frasnian age, is overlain by the Luxton Nodular Limestone which is thicker to the North and thinner to the South. In the early Famennian the Whiteway Slate is developed parallel to the Luxton Nodular Limestone to the North and the Gurrington Slate to the South. The Whiteway slate thickens southward and thins northward, succeeding the Luxton Nodular Limestone and at the closing of the *Platyclymenia Stufe* this slate had covered the limestones at the North, marking the end of the Luxton Nodular Limestone. The Whiteway slate is a purple, green and grey slate with associated siliceous and calcareous nodules. The slate occasionally bears some trilobites including *Cr*? *ensae*, *Cr*? *wocklumeriae*, *D*. *tripartitus*, *D*. *griffithides* and some proetids, together with ammonoids, ostracods and some other phyla. This slate ranges up to the *Gattendorfia* *Stufe* where it is overlain by the Winstow Chert. Fauna and lithology suggest a shallow basinal origin for this formation, peripheral to the Chudleigh schwelle.

3.8.6 The Viverdon Down succession (Whiteley 1981)

Some small exposures of Upper Devonian rocks were recently discovered by Whiteley (1981) within the Culm Measure shales and grit of the Viverdon Down area. A complete series from the *Clymenia* *Stufe* has been discovered from various localities. Some of these localities are fossiliferous, bearing some ammonoids, ostracods, conodonts, trilobites (including *Ph*. *wedekindi*, *D*. *griffithides* and some proetids) and some other phyla. Whiteley suggested that these Upper Devonian formations are of deltaic or submarine fan origin.

3.8.7 The Launceston succession (Column 2, text-fig. 3.1A, p.99f) (Selwood in House *et al* 1977)

The Lower Petherwin Beds are the base of the succession and consist of slate with ammonoid-bearing limestone and yield a fauna of the *hoevelensis* Zone. The Upper Petherwin Beds are less calcareous and contain some siltstones and sandstones with a brachiopod fauna, trilobites (including *Ph*. *granulatus* and *Ph*. (*Om*.) *accipitrinus*) are rare. The Stourscombe Beds which overly the Petherwin Beds are composed of nodular and thin-bedded cherts and slates, rich in clymenids of the *Wocklumeria* *Stufe*. These beds can be divided into two divisions, carrying the *endogona* and *paradoxa* subzones respectively.

Among the trilobites of the Stourscombe Beds are *Ph.* (*Om.*) *accipitrinus*, *Ph.* *granulatus*, *Ph.* *wedekindi*, *Cr?* *wocklumeriae*, *Cr?* *ensae*, *Dianops* ?*anophthalmus* and *Chaunoproetus* ?*palensis* (very righ in the sighted trilobites. The fauna of the *Gattendorfia* *Stufe* was found in the overlying beds, the Yeolmbridge Beds which consist of a series of slates, sandstones and limestones.

The fauna and lithology suggest that this succession was of platform origin, far away from the shoreline, but shallower than the Liverton-Bickington-Ilsington succession. The Rora Slate is equivalent to the Stourscombe Beds plus the upper Petherwin Beds and probably also the base of the Yeolmbridge Beds. The Lounston fossil band is equivalent to the Upper Stourscombe Beds.

3.8.8 *The North Devon Coast succession* (Column 1, table 3.3, p. 99f)

A complete shallow sea sequence from the Middle Devonian to the Carboniferous is recorded in the North Devon Coast succession but since most of the units do not carry any critical index fossils, their precise age is still uncertain. The Morte Slates (Frasnian), the Pickwell Down Sandstones and the Upcott Beds (Lower and Middle Famennian) have not yielded any critical zonal faunas. (Selwood *et* *al* in House (1977)). The overlying Baggy Beds belong to the *Clymenia* *Stufe* and lower *Wocklumeria* *Stufe* while the youngest Devonian is the Lower Pitton Beds of late *Wocklumeria* *Stufe* age (Selwood et al in House (1977)). The upper Pilton Beds mark the beginning of the Carboniferous. The only trilobite found in the upper Famennian of this succesion is *Ph.* (*Om.*) *accipitrinus* which is found in the lower Pilton Beds.

The lithology and fauna suggest an association of coastal, offshore and ?fluvial rocks in this area.

The Rora Slate is equivalent to the Upper Baggy Beds plus the Lower Pilton Beds.

3.9 Equivalent Upper Devonian in Europe and western U.S.S.R.

Marine facies of similar age to the Rora Slate can be observed in many places in Europe but few of them match, either palaeontologically or palaeoecologically, with the Rora Slate. However phacopid bearing formations with a similar stratigraphic range to the Rora Slate have been discovered from several localities in Europe especially in Germany where the research on these particular fossils was first commenced by systematic palaeontologists.

3.9.1 Germany

The German Upper Devonian can easily be divided into 3 major areas; the Rhenish Schiefergebirge, the Ostthüringen Schiefergebirge and the Harz Schiefergebirge (Erben & Zagora 1967).

The Rhenish Schiefergebirge - In this area the equivalents of the main part of the Rora Slate are the "Wocklumer Schichten" and the "Hangenberg Schiefer". The base of the Rora Slate might fall into the "Dasberg Schichten" below while the top of the Rora Slate is equivalent to the lower part of the "Hangenberg Kalk" of the Lower Carboniferous. The Lounston fossil band is comparable to the Upper Wocklumer Schichten, while the Combe fossil band could be placed somewhere in the Hangenberg Schiefer. The Upper Famennian of the Rhenish Schiefergebirge is usually very fossiliferous among which fossils are included phacopid trilobites. Phacopid trilobites were found in several localities in the districts of Balve, Iserlohn, Ruthen, Madveld, Dillenburg, Kellerwald and several other districts within the Rhenish Schiefergebirge (R. & E. Richter 1926, Schindewolf 1937, see table 3.4, p.110f). Ecologically the phacopids are closely associated with the "cephalopod limestone facies" or the "schwelle facies" in this area. The phacopid faunas here are a mixture of the well developed eye phacopids and the reduced eye phacopids as well as the blind ones.

The Ostthuringen Schiefergebirge - In this area the Rora Slate is equivalent to the upper "Clymenia Schichten" or the upper "Cypridinen Schiefer", but most of the phacopids are closely associated with the former. Most of the phacopid trilobites here are of the blind and reduced eyed fauna (Pfeiffer 1954, 1959; R. & E. Richter 1926, see table 3.4, p.110f). Among the fossiliferous localities where the phacopids were found are the Saalfeld, Gattendorf, Schleiz, Steinach and Schubelhammer localities; only in the last locality have the well developed eye phacopids been found. Phacopid trilobites were also found in the adjacent areas of Frankenwald and Schlesien (Silesia).

The uppermost Devonian of the Harz Schiefergebirge which consists of the "Cypridinen Schiefer" and the "Clymenia Kalk" of a locally developed "schwelle" rarely contains phacopid trilobites (see table 3.4, p.110f).

(Summaries on the distribution of phacopid species are shown in text-fig. 3.4, p.110f).

3.9.2 Upper Devonian elsewhere.

Some of the phacopids found in the study area were also found in NW France (Richter 1926, Hahn 1975), North France/South Belgium

→
Table 3.4
Text-figure 3.2

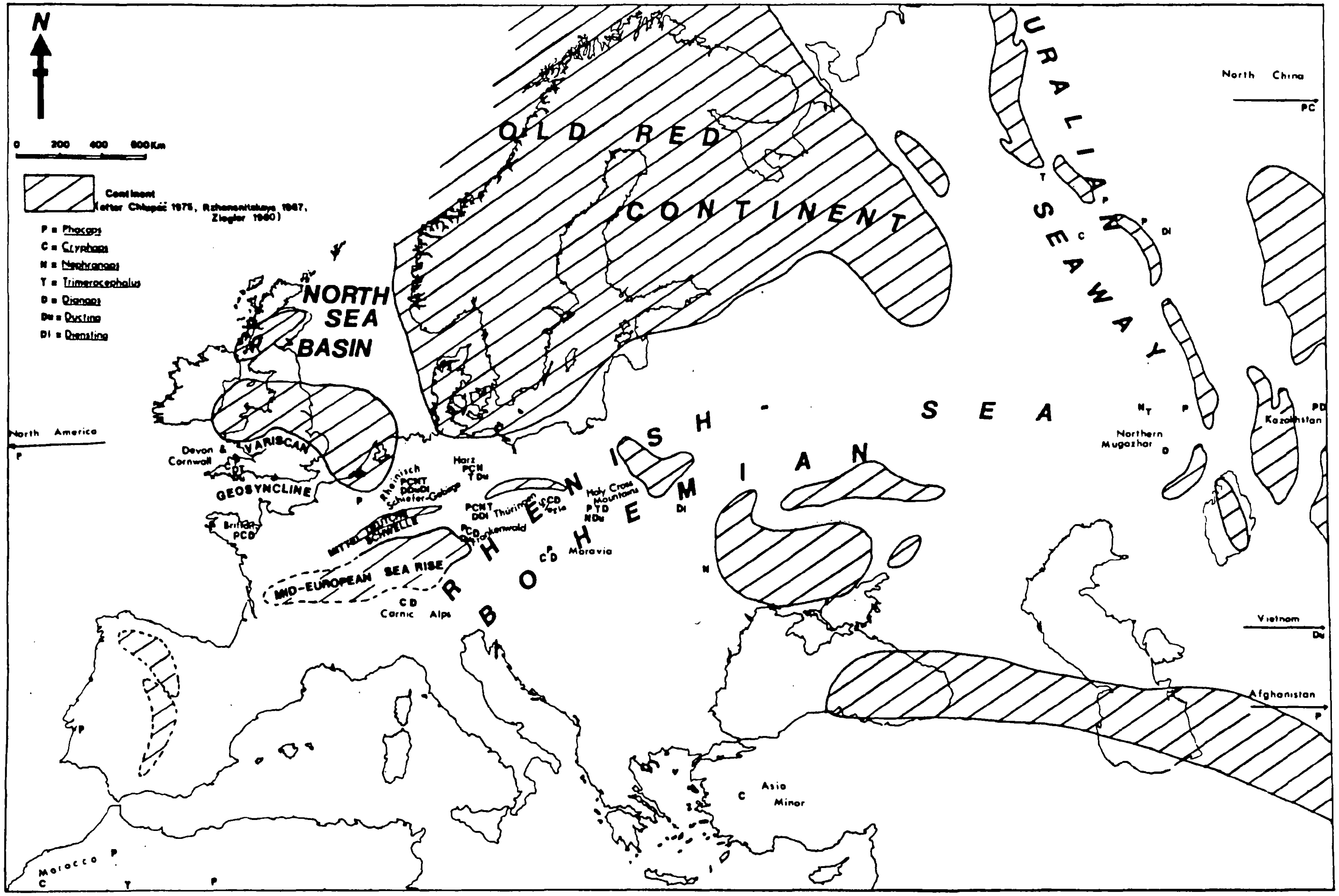
Table 3.4 The distribution of the Upper Famennian phacopid trilobites in Eurasia.

	Localities	1	2	3	4	5	6	7	8	9	10
	Morocco	*									
	Portugal		*								
	Kasakhstan	*									
	Ural Mountains		*	*				*			
	Carnic Alps				*	*			*		
	Moravian Karst		*	*	*						
	Holy Cross Mtns		*	*							
	Silesia		*			*			*		
	Frankenwald		*		*	*	*				
	*Ostthuringen		*		*	*	*	*	*		
	Harz Mtns		*								
RHENISH SCHIEFERGEBIRGE	*Kellerwald		*		*			*			
	Dillenburg		*		*			*			
	Barmen		*					*			
	Hattingen & Endorf							*			
	Hirschburg			*							
	Elberfeld		*								
	*Madfeld		*			*		*			
	*Rüthen		*	*				*			
	*Iserlohn		*	*	*	*		*	*		
	*Balve		*	*		*			*		
	N France & S Belgium	*									
	W France				*			*			
SW ENGLAND	Barnstaple	*									
	Launceston	*	*	*	*	*		*			
	Viverdon Down		*	*				*			
	NW Dartmoor				*	*					
	*Chudleigh	*	*		*	?		*	*	*	
	Liverton	*	*	*	*	*	*	*		*	*

Phacopid species

1. <u>Phacops</u> (<u>Omegops</u>) sp.
2. <u>Ph. granulatus</u>
3. <u>Ph. wedekindi</u>
4. <u>Cr? ensae</u>
5. <u>Cr? wocklumeriae</u>
6. <u>D. limbatus</u>
7. <u>D. griffithides</u>
8. <u>D. anophthalmus</u>
9. <u>D. tripartitus</u>
10. <u>D. combensis</u>

Chudleigh - Mt. Pleasant area (4), Winstow Cottage (1,2,7,8), Ideford area (?5,7,9).
Balve - Balve (2,5), Hönne-Tal (2,3,5), Effenberg (3,5), Dasberg (2,3), Albringen (2), Wocklum (5), Müsenberg (2), Humberg (2), Hövel (2), Trachtenberg (8), and ? Apricke (5).
Iserlohn - Apricke (3,4,8), Riemke (2,3), Höcklingsen (5,7), Seiler (2).
Rüthen - Kruhberg (2,3), Frankenburg (2,7), Drewer (2), Kallenhardt (2), Stillenberg (2).
Madfeld - Bredelar (2,7), Reischeider (5).
Kellerwald- Hauern (2,4,7), Ense (2,4,7), Branau (4,7).
Ostthuringen - Gattendorf (4,5,7), Saalfeld (4,5,6,8), Schleiz (4,6), Schübelhammer (2).



TEXT-FIGURE 3.2 : DISTRIBUTION OF PHACOPID TRILOBITES IN EURASIA DURING THE UPPER DEVONIAN after CHLUPÁČ 1975

(Richter 1933, Struve 1976). Poland (Osmolska 1958, Koscielniakowska 1967, Chlupac 1977^{ii}), Czechoslovakia (Chlupac 1966, 1977^{i}), Austria (Richter 1926) and Portugal (Richter 1926). (see table 3.1).

In the U.S.S.R. the same phacopids found in the study area are found in the Ural Region including the northern Mugodjar area, but they come from an older horizon (Maksimova 1955, 1980); the Lytva Horizon, which is equivalent to the Rora Slate and which is unfossiliferous (Breivel *et al* 1967). Central Kazakhstan marks the eastern limit of the phacopid trilobite distributions during the uppermost Famennian (do VI) where a few phacopids were found in the so-called "Transitional Beds" (Etroeungtian) (Maksimova 1980, Weber 1937).

The southern limit of the Upper Famennian phacopid realm is the Tafitalt and Central Morocco of North Africa (Alberti 1972, Struve 1976).

3.10 Summary

The critical index fossils indicate that the Lounston fossil band has an age equivalent to the *sphaeroides* subzone (do VIβ) of the Famennian while the Combe fossil band is slightly younger, having an eye equivalent to the *euryomphala* Zone (do VIβ) of the Famennian. The upper and lower boundaries of the Rora Slate were not determined during this research, but all the fossil collections from this formation, particularly the phacopid trilobites, agree with the limit suggested by Selwood in House (1977) i.e. upper *Clymenia Stufe* (do V) for the bottom and lower *Gattendorfia Stufe* for the top of this formation.

The main localities of the study area are equivalent to the Stourscombe Beds of Launceston, to the Upper Mount Pleasant Group of Chudleigh and to the Lower Pilton Beds of North Cornwall. In continental Europe the Lounston fossil band is equivalent to the upper Wocklumer Schichten while the Combe fossil band is equivalent to the Hangenberg Schiefer of the Rhenish Schiefergebirge. In the Ostthuringen Schiefergebirge the Rora Slate is equivalent to the upper "Cypridinen Schiefer" or the upper "Clymenia Schichten".

The phacopid trilobites of the study area and those of elsewhere in England and Europe share the same stratigraphical range.

CHAPTER 4

PALAEOECOLOGY

4. 1 Introduction

According to Selwood (in House et al 1977) the Rora Slate is of basinal origin, as indicated by its lithology and fauna, and includes green and dark purple slates with thin limestones and siliceous nodules, together with the calcareous siltstones of distal turbidite origin which form the Upper part of this formation.

Recent data indicate a mixture of shallow and deep water fauna, with widespread "ostracod slates" indicating the basinal origin of the area; shallower parts of the basin, one of which is the study area, are indicated by a specialized shallow water fauna mixed in with the omnipresent ostracods. Detailed discussion on this subject will be the main theme of this chapter.

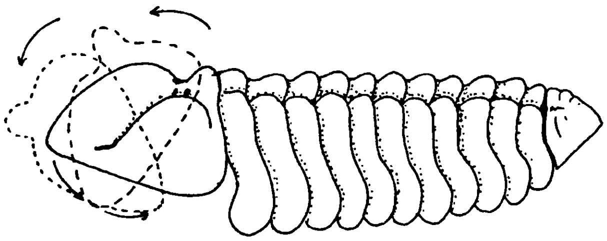
4. 2 "Biocoenosis" and "Salterian Moult"

It is important to note that the fauna discussed in any palaeoecological study should represent a "biocoenosis" or living assemblage, otherwise the discussion is meaningless. Two main lines of evidence have been used in this study to prove the presence of a "biocoenosis" in the studied area. These are the presence of close, intact or scarcely shifted valves of bivalves and more importantly the presence of the "salterian moult" in phacopid trilobites. Other evidence which is also used includes the intact dead trilobites, both in phacopids and proetids, and the presence of the rootlets of solitary corals. The above evidence strongly suggests that the depositional environment of this formation was very quiet, thus the benthic faunas should represent a biocoenosis or a living assemblage at the time of the deposition. (see table 4.1, p.116 for details of the biocoenosis evidence of every locality studied.

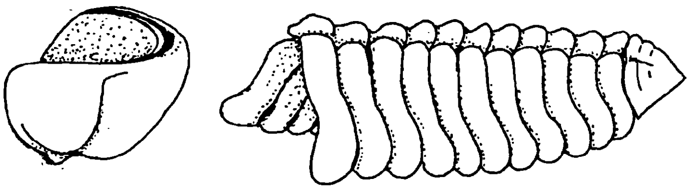
The "salterian moult" is a common mode of ecdysis among the trilobites with non-functional sutures especially in the family Phacopidae. It is also called the "phacopid moult", (Harrington <u>et al</u> in Moore 1959). During moulting a trilobite with a non-functional suture got out of its old exoskeleton by using the line of weakness between the cephalic exoskeleton and the first tergite of the thoracic exoskeleton. When performing this, the animal pushed its cephalic exoskeleton forward by holding the thorax and pulling the anterior cephalic exoskeleton backward. The cephalic exoskeleton then parted from the thorax and finally overturned, at which point the animal could move out freely from its former exoskeleton, leaving the thorax and pygidium in normal life position (see text-fig. 4.1, p.115) for further details. The presence of the salterian moult in the study area indicates that there was no disturbance (post moulting) in this depositional environment. Thus, this can offer help in determining the actual bedding plane where it is not easily discernable, and can also be used in determining the overturned layer. Text-figure 4.1b exhibits the salterian moult on a true layer, where as in an overturned layer a reverse situation (i.e. the cephalon is in life position while its thorax and pygidium are overturned) should be expected.

In the study area, the salterian moult is very common among the blind phacopids (see pl. 3 , fig. 11 and pl. 4 , fig. 10&12).

Beside the salterian moults, the intact dead phacopids also reflect the calmness of the depositional environment. However, the activities of a very weak current can be interpreted by the presence of phacopid cephala preserved in life position together with the rest of their exoskeleton but not intact, though sometimes very close to each other. Two possible origins of this situation are the post-mortem disintegration or the post-moulting reorientation of the cephala.



a. the moulting process



b. the "salterian moult"

Text-figure 4.1

Common process and mode of moulting in the studied phacopids

note:

1. The palaeoecology of the Rora Slate will only be discussed in detail for two main localities i.e. the Lounston fossil band and the Combe fossil band. The other localities are only supplementary and will be discussed briefly in connection with the trilobites, especially the phacopids.

2. In the main localities, the discussion will be concerned more with the phacopid trilobites than the others.

Table 4. 1 Trilobite compositions and biocoenosis evidence in the study area

Locality		phacopids		proetids		S.M.	i.d.	biv.	c.r.
		V	B	V	B				
Lounston fossil band	1A	*	*	*	*	*	*	*	-
	1D	*	*	-	*	-	*	*	-
	1B	*	*	-	-	-	-	-	-
	1C	*	*	-	*	*	*	*	-
Combe fossil band	2	-	*	*	-	*	*	*	-
Ramshorn Down terrace	3	*	-	-	-	-	-	-	-
Rora trench	4	-	*	-	-	-	*	-	-
Lounston Farm II	5	*	*	-	-	-	-	*	-
	6	-	-	-	*	-	-	-	-
Combe II	7	-	*	-	-	-	-	-	-
	8	-	*	-	-	-	-	-	-
	9	*	-	-	-	-	-	-	-
	10	-	*	-	-	*	-	-	-
Liverton	11	-	*	-	-	-	-	*	-
Combe Farm track	12	-	*	-	-	*	-	-	*
Langmead Farm	13	-	-	-	*	-	*	-	-

V= sighted trilobite B= blind trilobite S.M.= salterian moult
i.d.= intact dead trilobite biv.= intact bivalve c.r. = coral rootlet

4. 3 PALAEOECOLOGY

Apart from their diversity, the general structures of the palaeocommunities of the Lounston and Combe fossil bands are very similar. They both have the same form of benthonic, planktonic and nektonic features, but the diversity of the fauna of the Lounston fossil band is much higher than that of the Combe fossil band.

Their benthic faunas consist mainly of epifaunal forms which can be divided into two groups, the sessile suspension feeders and the vagrant substrate feeders. The bivalves with elongated valves might live as infaunal burrowing forms, but no evidence of burrowing has been found.

The sessile benthos are similar in both fossil bands and consist of brachiopods, solitary corals, crinoids and perhaps some bivalves. The bryozoans were only found in locality 1B of the Lounston fossil band. The vagrant benthos consists of trilobites.

The nektonic faunas in both Lounston and Combe fossil bands consist of clymenids. The planktonic faunas are made up of ostracods with well ornamented shells, while the thin shelled bivalves probably represent the pseudoplanktonic faunas of the study area.

4.3.1 The Lounston fossil band

Three fossiliferous localities were discovered in this fossil band during this study, and were named locality 1A, 1B and 1C positioned from bottom to top (see text-fig. 1.2b). The supplementary locality 1D was discovered by Waters in 1971 and was situated between locality 1A and 1B, also shown on the same figure.

In general the diversity of the faunas decreases from bottom to top, and they will be discussed in the following pages.

a) The locality 1A

The sessile benthos are rare compared to the vagrant benthos at this locality. The sessile fauna is made up of brachiopods, solitary corals, crinoids and probably some bivalves. This fauna is left unclassified in my collection. The vagrant fauna is formed by a mixture of trilobites with well-developed eyes and blind forms. They are *Phacops granulatus*, *Ph. wedekindi occidentalis*, *Ph. wedekindi microps*, *Ph. wedekindi* ssp. A, *Cryphops*? *wocklumeriae lounstonensis*, *Dianops limbatus*, *D. griffithides griffithides*, *D. tripartitus*, *Typhloproetus subcarintiacus*, *Ty. ?microdiscus*, *Chaunoproetus palensis*, *Ch. carnicus*, *Ch. tietzei*, *Drevermannia schmidti* and *Cyrtosymbole* sp. indet.. This trilobite assemblage indicates that their environment must have been very rich in food and lacked predators. Enrolled specimens are very rarely found. Enrolment in trilobites is usually connected with the protection of their soft underbodies against predators or enemies, (Harrington *et al* in Moore 1959). In the study area there is no complete "phacopid type" enrolment to be found, but broken, partly enrolled specimens are occasionally found though very rarely.

The nektonic fauna includes the clymenids of the genera *Cymaclymenia*, *Kosmoclymenia*, *Cyrtoclymenia*, *Epiwocklumeria*, *Kalloclymenia* and ?*Postglatziella*. This fauna is comparatively less diverse than the benthic fauna. The planktonic fauna is very rich and was represented by the ostracods including *Richterina* (*R.*) *striatula*, *R.* (*R.*) *costata*, *Maternella hemispherica*, *M. dichotoma*, and ?*R.* (?*Fossirichterina*) *intercostata*. The bivalves which have small and thin shells represent the pseudoplanktonic fauna.

b) The locality 1D

Except for the phacopid trilobites, the other members of the fauna have not been studied in detail. The phacopids consist of *Ph. granulatus*, *Ph. wedekindi occidentalis*, *Cr*? *ensae*, *D. griffithides griffithides*, *D. tripartitus*, *?*D. combensis* and *D.* sp.A. Beside these phacopids there are some blind proetids, brachiopods, solitary corals, bivalves and crinoids in the benthic community of this locality. The nekton includes the clymenids, while the plankton consists of ostracods and the pseudoplankton is represented by the thin-shelled bivalves.

note: *? The rocks carrying this species are very different in nature from the other rocks at Lounston. Possibly these rocks and their fossils came from other localities of the Rora Slate and were mixed up during the numbering process by the collector (i.e. Dr. R. Waters).

c) The locality 1B

The benthonic fauna of this locality is very poor compared to the other localities at Lounston. The trilobites consist of *Ph.* sp. indet. (pygidium), *D. griffithides griffithides* and *D.* sp.A. Among other benthos are brachiopods, solitary corals, crinoids and bryozoans. This locality is rich in nektonic fauna which consists of the clymenids from the genera *Cymaclymenia*, *Kosmoclymenia*, *Cyrtoclymenia* and Kenseyoceras. The planktonic fauna here is not as rich as in the other localities at Lounston, and it includes the ostracods *R.* (*R.*) *striatula*, *R.* (*R.*) *costata* and *M. dichotoma*. The pseudoplankton is represented by the thin-shelled bivalves.

d) The locality 1C

The benthos of this locality is poorer than that of the locality 1A. The vagrant benthos include *Ph.* sp. indet. *D. tripartitus*, *D. griffithides griffithides*, *D. limbatus* and *Ch.* sp. indet. The sessile benthos include brachiopods, solitary corals, crinoids and bivalves. The nekton consists of the clymenids of the genera Cymaclymenia and Kosmoclymenia only. The planktonic fauna of this locality consists of ostracods including *R.* (*R.*) *striatula*, *R.* (*R.*) *M. hemispherica* and *M. dichotoma*, and the pseudoplankton is made up of thin-shelled bivalves.

→ table 4.2

Table 4. 2 The occurrence of phacopid trilobites in the Lounston and Combe fossil bands.

Species Lists	The Lounston fossil band						Combe fossil band	
	Locality 1a		Locality 1d (all unweighed)	Locality 1b (all unweighed)	Locality 1c			
	Weighed (91 Kg)	Total (incl. unweighed)			Weighed (19 Kg)	Total (incl. unweighed)	Weighed (84 Kg)	Total (incl. unweighed)
Ph. granulatus	6	9	1	-	1	-	-	-
Ph. wedekindi occidentalis	9	11	1	-	-	-	-	-
Ph. wedekindi microps	12	17	1	-	-	-	-	-
Ph. wedekindi ssp. A	-	2	-	-	-	-	-	-
Cr? wocklumeriae lounstonensis	14	18	-	-	-	-	-	-
Cr? ensae	-	-	2	-	-	-	-	-
Cr? Sp. A	-	-	1	-	-	-	-	-
Total sighted phacopids (phacops + Cryphops)	49	67	7	-	1	2	-	-
D. limbatus	4	7	-	-	1	1	-	-
D. griffithides griffithides	5	7	1	1	5	8	-	-
D. tripartitus	6	8	-	-	1	3	-	-
D. combensis	-	-	3	-	-	-	80+	130+
D. Sp. A	-	-	1	1	-	-	-	-
Total of blind phacopids	15	22	5	2	7	12	80+	130+
Total phacopids	64	89	12	3	8	14	80+	130+
Ratio (sighted:blind)	7:2	3:1	7:5	1:2	1:7	1:6	All blind	All blind

e) The environmental change and the distribution of the phacopids

Generally the decrease in the diversity of the benthos, from the bottom to the top of this fossil band reflects an environmental change which is unfavourable to some of the benthos. This change seems to be parallel to the faunal change in the phacopid trilobites. At the bottom of this fossil band the phacopids with well-developed eyes are abundant but toward the top their occurrence and diversity decrease strongly. Meanwhile, the blind phacopids although they do not increase in species number, do increase in the number of occurrences from bottom to the top of this fossil band. The change which is in favour of the blind trilobites in the Upper Devonian is usually connected with the increase in depth, Clarkson (1967). The proetids are very rare in this fossil band, but where they are abundant (i.e. at the locality 1A), most of them (i.e. nearly 100%) are blind. The sighted proetids have never been found in this fossil band, except at the locality 1A. For further comparison see table 4.2, p.119f).

4.3.2 The Combe fossil band

This fossil band is an example of a specialized fauna, indicated by a very low diversity with a major species dominating the others. This major species is Dianops combensis n.sp., also representing the only phacopid species in this fossil band. Their number of occurrences reaches nearly 90% of the total benthos of this fossil band. The other members of the benthos are the proetids (?Archegonus sp.), brachiopods, solitary corals, crinoids and bivalves. An assemblage like this is usually connected with an environment which has low nutrient levels, so that only the species with some special feeding habit can dominate. The trilobites as a dominant species indicate that most of the nutrients are in the substrate, and since this species is blind, the environment is likely to be a dark one.

The nektonic fauna is very poor compared to the benthos and is made up of only *Cymaclymenia euryomphala*. The planktonic fauna is also very poor compared to that of the Lounston fossil band. Components of this fauna include the ostracods *M. hemispherica*, *R.*(*R.*) *striatula*, *R.*(*R.*) *costata* and *R.*(*F.*) *semen*. The thin-shelled bivalves are rare and represent the pseudoplankton.

4.3.3 The other localities

- the localities 3-10 studied from Waters' collections
- the localities 11-13 studied from present author's collections

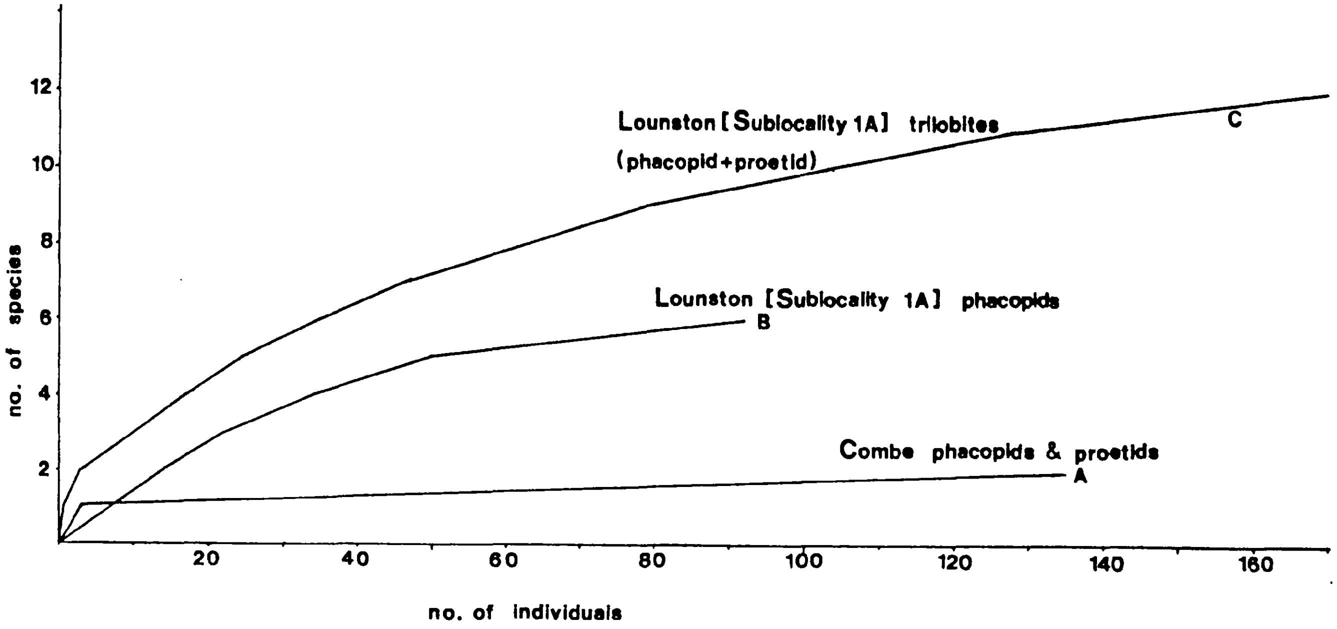
Only 3 of these localities contain phacopids with well-developed eyes. They are locality 3 with *Ph. granulatus*, locality 5 with *Ph. wedekindi ?occidentalis* and locality 9 with *Ph.* (*Om.*) sp.B. The blind phacopids can be found at all localities except the localities 3, 6, 9 and 13. *D. combensis* was found at locality 4, while *D. ?limbatus* was found at locality 10 and *D.* sp. A at locality 5. The other *Dianops* from other localities cannot be classified into the species rank since they lack cephalic details. Remains of blind proetids were found at localities 6 and 13. The other components of the fauna were not studied in detail.

4.3.4 Sediment/fauna relationships

(see text-figure 4.2, p. 121f).

Slates with nodules in locality 1A are accompanied by a very diverse benthos while the pure slate localities (e.g. localities 10 and 2 on the other hand, possess a very poor benthonic fauna with abundant blind

⟶
text-figure 4.2



Text-figure 4.2 : Rarefaction curve for the main localities studied phacopids. The above observations suggest that the slates with nodules contain very high nutrient levels while the pure slates are poorer in nutrients. Since the slates with nodules also possess phacopids with well developed eyes, it might also indicate relatively shallower water compared to the pure slate where the phacopids with well developed eyes are very scarce.

Furthermore, the Dianops seems to have very special feeding habits so that it could survive in areas of high or low nutrient levels.

4.3.5 The effect of Famennian/Lower Carboniferous transgression on the fauna of the study area

At the top of the Rora Slate, there is evidence of the transgression which marks the end of the Devonian period. This evidence concerns the studied fauna, especially the phacopid trilobites.

Generally toward the top of the Rora Slate (upper part of VI of the Famennian) the numbers of benthic animals decreased. In the case of the phacopids this decrease in the benthos strongly affected the sighted members of this family (see table 4.2, p. 119f). The sighted phacopids decrease toward the top of this formation as the other benthos decrease. The blind phacopids did not change very much until the topmost levels of the Rora Slate where they were rapidly reduced. At locality 2, very close to the top boundary of the Rora Slate, the sighted phacopids are absent while the only blind phacopid species present becomes a major species here. Brachiopods and corals are rare here and they probably represent the survivors from shallower water stock.

4.3.6 Comparisons of the phacopid fauna

* The distributions of phacopids species during the Upper

Famennian (do V - do VI) in Eurasia are tabulated in table 3.4, p. .

* The distribution of the Upper Devonian phacopid genus are figured in text-figure 3.2, p.110f

The phacopid faunas of the study area were compared with phacopid faunas elsewhere in England, Europe and the U.S.S.R. (see table 3.2, p. 110f). From that table it may be seen that no other areas match perfectly with the study area, but some of them are closely similar to it. In the SW England, there are no other areas which contain richer blind phacopid faunas than that belonging to the study area. The sighted phacopid faunas of the study area however, are similar to those from the Chudleigh and Launceston areas, except that Ph. wedekindi s.l. has never been found in the Chudleigh area. As well as a richness in blind phacopids the study area is also rich in blind proetids which are poorly represented in other areas of SW England.

In mainland Europe there are some areas which have phacopid faunas closely similar to those of the study area (see table 3. 2, p. 110f). They are the "Rheinische-Schiefergebirge" or the Rhenish mountains (represents the "schwelle" or submarine rise facies) and the Thuringia area (represents the "becken" or basinal facies) of Germany. The Rhenish Mountains has a similar sighted phacopid fauna to those of the study area but the blind phacopid faunas of the former are poorer compared to the latter. The blind phacopid faunas of the Rhenish Mountains consist of only D. griffithides and D. anopthalmus while in the study area D. griffithides was found together with D. limbatus, D. tripartitus and D. combensis (D. anophthalmus is absent). In Thuringia, the diversity of the blind phacopid faunas is similar to those of the study area, although they consist of different species. The sighted phacopids appear to be poorer in the Thuringia area compared to those of the study area (see table 3.2,p.110f). It seems that the faunas of the study area are a mixture of the faunas of the Rhenish Mountains and Thuringia. All these areas, i.e. the Rhenish Mountains and Thuringia have a similar blind proetid fauna to those of the study area, and furthermore these German areas are also very rich in the sighted proetid faunas. The other European phacopid faunas (see table 3.2,p.110f), are very poor compared to the faunas of the study area. The Russian faunas are also very poor compared to the studied faunas. (For more details see table 3,2, p.110f).

In consequence of the above comparisons, the following conclusions were drawn:

1. The Upper Devonian phacopids should be divided into 2 major groups (i.e. the blind and the well developed eyes) according to their characters and behaviour.
2. Blind phacopids represent a deeper water environment (basinal facies) (Clarkson, 1967) and well developed eye phacopids represent a shallower water environment (outer shelf facies).
3. The blind phacopids might occur (in a low proportion) in the shallow water environment (e.g. the Rhenish Mountains, Chudleigh and Launceston areas) while in an opposite case the well developed eye phacopids are occasionally found in the deep water environment, as in the Thuringia, Frankenwald and Silesian areas.
4. In extremely shallow water the specialization is more obvious where in many places (e.g. the Barnstaple area of N Devon, the N France, S Belgium, Morocco, Portugal and Kazakhstan areas) only

one or two species of phacopids with very well developed eyes occur. An extremely deep water environment is very rarely found but in W France and the Carnic Alps area there are examples of quite deep environments where only blind and reduced-eye phacopids were found.

5. The reduced-eye phacopids, as intermediate forms between the blind and the well-developed eye group, are usually found in a transitional environment i.e. the environment in which the water is not extremely shallow or deep. This group includes the genus _Cryphops_ and some subspecies of _Ph. wedekindi_.

6. The richness in the blind phacopids and the presence of some well developed eye phacopids, as well as the reduced-eye form in the study area, suggests that its depositional environment is quite deep (but not extremely deep). The bathymetry of the study area will be discussed in the next topic.

4. 4 The lithology, fauna and bathymetry

Most of the fossiliferous rocks in the study area are slates of various colours. Bluish or greenish-grey slates are found at the localities 1, 5, 11 and 13, while light coloured (yellowish-brown or light green) slates are found at localities 2,3,4,6,7, and 12. The slates at locality 1 bear some decalcified nodules, some of which are fossiliferous; while at locality 11 some unfossiliferous siliceous nodules are found. Fossils from localities 9 and 10 were found in a thin limestone layer.

The lithology and the faunas of the study area reflect aspects of both the shallow water and deep water environments.

All ostracods found in Rora Slate are of pelagic type and indicate a depositional environment which is below the photic zone (House 1975[ii]), and the absence of coarse terrestrial materials indicate that the depositional environment must be far away from the shore and free from turbidite and lateral sedimentation. This is supported by the presence of phacopid salterian moults and intact bivalves. The rich, blind phacopid faunas also indicate a deep water environment (Clarkson 1967) for the study area.

However other data seems to indicate a shallow water origin for the Rora Slate. The rich benthonic fauna (excluding the blind phacopids and proetids), especially the brachiopods, solitary corals and well developed eye phacopids indicates a shallow water environment. The presence of decalcified nodules and thin limestone layers also show that the depositional environment of the Rora Slate is quite shallow. The presence of a salterian moult in the limestone at locality 10 proved that the limestone layer was deposited <u>in situ</u> by contemporaneous vertical sedimentation of pelagic calcareous materials. The absence of volcanic activity could also indicate a shallow water environment, because according to Tucker (1974) the Upper Devonian volcanic activity usually took place in a deep water environment.

The composition of the benthos in the Rora Slate suggests that its depth of deposition might be at the same level as the Chudleigh submarine rise, but deeper than the Launceston outer-shelf; while the thick ostracod slates suggest that the depositional environment of the Rora Slate might be deeper than both the Chudleigh submarine rise and Launceston outer shelf. However the consistency of the "ostracod slates" in the basinal facies elsewhere (House 1975[ii], Krebs 1979) indicates that the Rora Slate was deposited in the basin. Whether it is deeper or shallower than the Chudleigh submarine rise is not known, but it is evidently deeper than the Launceston outer-shelf. The palaeogeographical position of the Rora Slate during its time of deposition will be discussed in the next chapter.

4. 5 Conclusions

The "salterian moult" of phacopids and the intact shells of bivalves which are very frequently found in the study area, as well as the rare coral rootlets, indicate a very calm depositional environment for the study area, therefore the faunal assemblages present here can be assumed to be a "biocoenosis".

The faunal differences in the main localities studied are due to the Famennian/Lower Carboniferous transgression and are also related to the sediment type. The sighted phacopids are more abundant in localities where decalcified nodules are present, while blind phacopids are more abundant in localities with pure slate.

In comparison to other phacopid faunas elsewhere, the studied phacopids represent a fauna of deep water (but not extremely deep) environment. Since the "ostracod slates" have consistently marked the basinal environment (House 1975^{ii}, Krebs, 1979), then the depositional environment of the study area should be in the basin. The location of the study area in this basin will be discussed in the next chapter.

CHAPTER 5

PALAEOGEOGRAPHY

5. 1 Introduction

Since there is no direct evidence on the palaeogeographical position of the study area, a comparison between the fauna and the lithology of this area and the surrounding areas is necessary in order to construct its palaeogeography. A brief summary of this account and the following discussions are shown in text-figure 3.1c, p. 99f and text-figure 5.1, p.131f. The model of the Upper Devonian marine facies distributions by House 1975[ii] has provided the basis for the study.

5. 2 Local palaeogeography

The faunas and lithology of the study area characteristically belong to the Hercynian (basinal) Magnafacies, however the presence of a later, shallow water benthos suggests that the foundation on which the Rora Slate was deposited is of a shallow water facies. Since the foundation of the Rora Slate is absent (see text-fig. 3.1a, p.99f), there is no direct evidence to prove the above suggestion, but evidence of the late Clymenia/early Wocklumeria Stufen regression which is marked by the incursions of shallow water facies into N Devon and N Cornwall (House, 1977) might indirectly support the presence of a shallow water foundation for the Rora Slate. Further discussions on the palaeogeographical position of the study area will be the main theme of the rest of this topic.

5.2.1 Relationships between the study area and the Launceston and Chudleigh areas

Faunally and lithologically, the study area is of deeper water origin than the Launceston area.

Although in a lithological sense the study area appears to be of deeper water origin than that of Chudleigh, the evidence of the faunas of the two areas suggests that they may both be at the same level - that of relatively shallow water.

Hosever the faunal differences between the study area and the Chudleigh area strongly suggest that they are geographically separated. The brachiopods and solitary corals which frequently occur in the study area (abundant in some localities) are not found in the vicinity of Chudleigh at that time (i.e. do VI of the Famennian). Also absent in the Chudleigh area are _Ph. wedekindi s.l._ and the proetids. The geographical barrier between these two areas is probably a deep basin because theoretically the brachiopods and solitary corals will also be present in the "cephalopod limestone facies" if they are present in the nearby "ostracod slates". This fact militates against the possibility of the study area being deposited peripherally to the Chudleigh submarine rise, thus this submarine rise cannot be the origin of the shallow water benthos of the study area. Other possible origins of this shallow water benthos are an isolated submarine rise (other than the Chudleigh submarine rise) or the outer shelf.

note: One small solitary coral has been discovered in the Chudleigh area (House and Butcher, 1973). Instead of having brachiopods and solitary corals, the Chudleigh area contains quite numerous gastropods and the benthic bivalves (ibid.).

5.2.2 The drowned submarine rise

The fauna of the study area has some characteristics in common with the fauna to be found on the Chudleigh submarine rise. This leads to the suspicion that the study area may have been situated on a comparable structure. This hypothesis would favour the origin of the new local species, *D. combensis* and subspecies, *Ph. wedekindi occidentalis* and *Cr. wocklumeriae lounstonensis* which might thus result from the total isolation of this area. However such a hypothesis is rendered untenable because there is no lithological evidence of a submarine rise to support the palaeontological evidence.

5.2.3 The drowned outer shelf

The sessile benthos of the study area are similar to those of the Launceston (outer shelf) area, thus suggesting that these two areas may have a connection with one another and the foundation of the Rora Slate was once an outer shelf.

In this hypothesis, some of the sighted phacopids, brachiopods and solitary corals of the Rora Slate may be ecologically predisposed to the deeper waters induced by rapid transgression while few sighted phacopids might manage to move into shallower waters. The phenomenon seen in the Lounston fossil band where the number of occurrences of sighted phacopids decrease upward in this local succession (see table 4.2, p.119f),perhaps resulted from the migration of these faunas to the shallower places as the water became continuously deeper. The brachiopods and corals as they are sessile benthos, stayed there until the water became too deep for them. The new species and subspecies (see above, 5.2.2) found in the Rora Slate may be derived from an unknown place, since this hypothesis does not favour the introduction of new species.

In the same way as the first hypothesis the latter is also ultimately untenable, although the more probable, due to lack of evidence on the presence of the outer shelf foundation of the study area. Further study on the base of the Rora Slate is crucially important in order to construct a more tenable palaeogeographical picture of the study area.

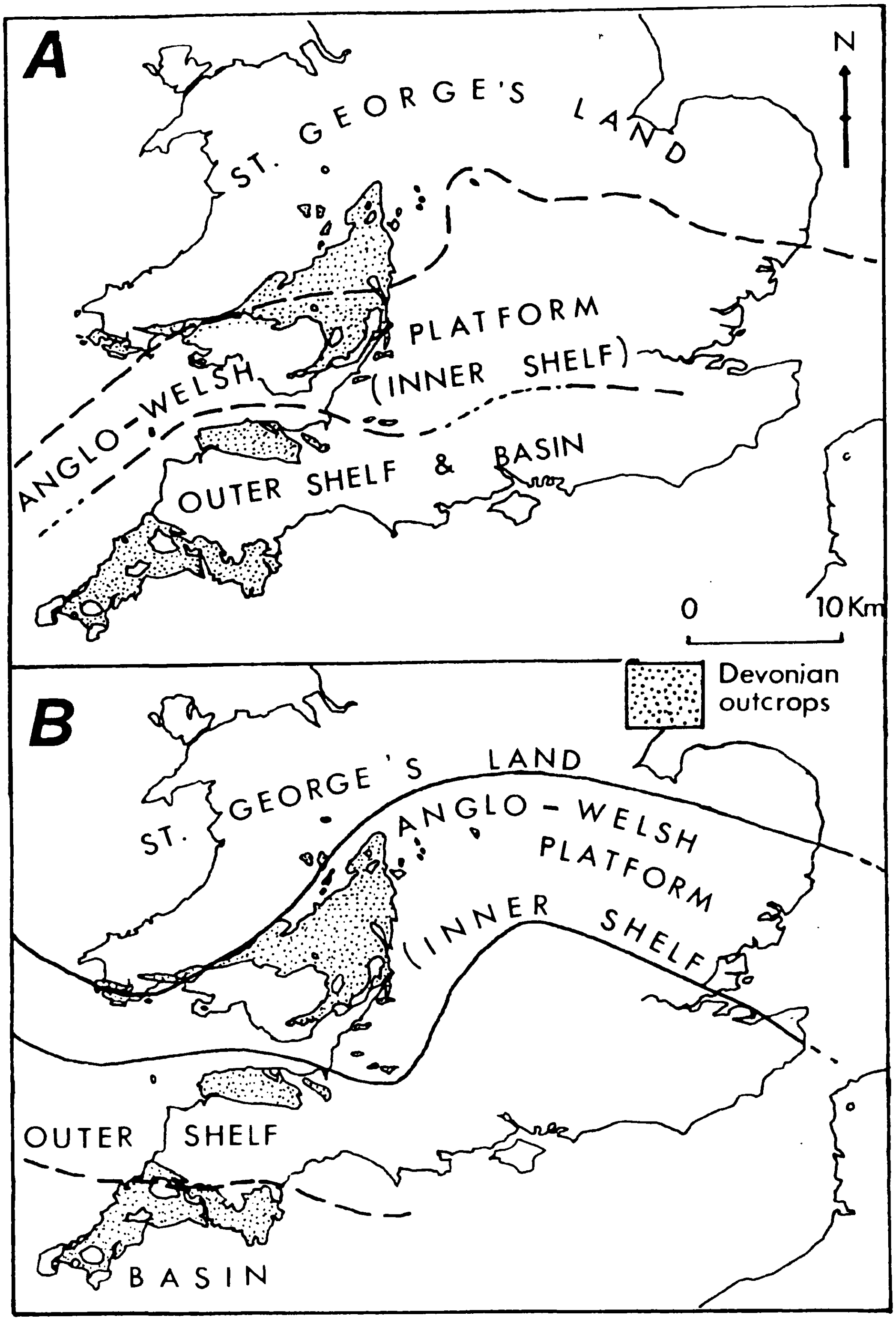
5. 3 The palaeogeography of the SW England

In the Upper Devonian there are three major facies which are very important in indicating the major geographical areas. These facies are the Old Red Sandstone (continental) facies, the Rhenish (shallow marine includes the reefs and the outer shelf) Magnafacies and the Hercynian (deep water includes the submarine rise and basin) Magnafacies.

All the major facies can be seen in outcrops in Wales and SW England while towards eastern England the Upper Devonian deposits are concealed. As in the other parts of North Europe the Old Red Continent was situated to the North, while the basin was to the South. Without the aid of borehole data, the reconstruction of the palaeogeography of the Upper Devonian is impossible to complete.

The reconstructed shoreline of the Frasnian transgression by Butler (1981)(see text-fig. 5.1a) runs in an East-West direction through Cambridgeshire and Warwickshire in England. In South Wales the shoreline runs in much the same direction as mentioned above, but lies a little further South. North of this shoreline is the St. George's Land (the Old Red Continent), while South of it is the marine Rhenish Magnafacies. Allen (1979) draws a further northward shoreline in the later Devonian (close to the Devonian/Carboniferous boundary)(see text-fig. 5.1b, p.131f). He was also able to reconstruct the basin/platform boundary, this boundary

⟶
text-figure 5.1



Text-figure 5.1 :

Setting of the continental and marine deposition during the Upper Devonian times in Southern Britain

A. During the Frasnian Maximum Transgression (after Butler 1981)

B. During the late Famennian times (after Allen 1979) being parallel to the shoreline and far out to sea in East and Central England, but closing with the shoreline to the West, leaving the North Devon deposits in the basin. But as described by Krebs (1979) and House (1975b) in terms of Hercynian or Rhenish Magnafacies, these North Devon deposits are still classified into the Rhenish Magnafacies as are the North Cornwall deposits (at least until the upper Wocklumeria Stufe age). The present evidence indicates that the Rhenish/Hercynian Magnafacies boundary could lie somewhere just slightly North of the study area in South Devon and between Launceston and Viverdon Down in Cornwall. North of this boundary line in North Devon and North Cornwall the Rhenish (outer shelf) facies was deposited. Earlier, in the middle Famennian and early upper Famennian, regressional events led to incursions of inner-shelf facies across this area, reaching the Launceston district in the early upper Famennian. However towards the end of the Famennian, the outer shelf facies was again re-established. South of this boundary line, in South Devon the basinal facies was well developed except for several small faulted blocks in the Kate Brook succession which was suggested by Selwood in House 1977 as having an outer shelf origin. The mixed shallow and deep water faunas at the study area might indicate a transition between the Rhenish and Hercynian Magnafacies. Generally, the Hercynian Magnafacies in South Devon is very similar to that established in the Rhenish Mountains of Germany. It consists of both submarine rise or "schwelle" facies and basinal or "becken" facies. In South Devon the submarine rise facies is present in the Chudleigh area and from here, southward, there is a continuation of facies changes from the shallow submarine rise facies to the deep basinal facies. In Cornwall, a recently found Hercynian facies in the Viverdon Down area (Whiteley 1981) placed the Rhenish/Hercynian Magnafacies boundary in between this area and the Launceston area.

The reconstruction of the shoreline, the continent and the basin in the southern part of Great Britain is closely related to other parts of northern Europe.

5. 4 European Palaeogeography

In northern Europe, the Old Red Continent was situated at the North while the Rhenish-Bohemian Sea was situated to the South. St. George's Land which is seen in N Wales and the Midlands in Great Britain, formed part of the Old Red Continent in most of the Devonian Times, but as Carboniferous times approached the Old Red Continent began to split up. St. George's Land in the uppermost part of the Devonian formed an island which extended eastward to Belgium and Holland and was separated from the main Old Red Continent by a North Sea embayment (Ziegler 1980). The main Old Red Continent, East of this sea consists of Denmark, the Scandinavian landmass, the Baltic Sea and the northwest part of the U.S.S.R. (see text-fig. 3.2, p. 110f).

The Variscan Geosyncline in England is continued by the Hercynian Geosyncline in northern Europe. A similar facies distribution as seen in England can be observed in S Belgium, N France, West and East Germany. The shallow Rhenish Magnafacies can be seen in S Belgium and N France, which resemble closely the N Devon area of SW England, where only very well developed eye phacopids are present. The deeper part of the Rhenish Magnafacies in N France and in the western Rhenish Mountains were concealed and parts of the area eroded (House 1975[i]), so that there is no representative facies equivalent to the Launceston area of N Cornwall and to that of the study area. The Hercynian Magnafacies is well developed in West and East Germany where the terms "schwelle" (submarine rise) and "becken" (basin) are well established (House 1975[i], Krebs 1979, Paproth & Streel 1970). In the eastern Rhenish Mountains the "cephalopod limestone facies" is well developed on several submarine rises of different origins[*1] (Tucker 1976), within the vicinity of the "ostracod shales facies". The phacopids occur randomly and usually in the "cephalopod limestone facies" within this area. The analogy of this area in SW England is the Chudleigh area where similar forms of phacopid trilobites are found. In the Thuringia-Frankenwald area the deeper "basinal facies" are found where the "cephalopod limestone facies" is absent and the phacopids usually occur in the "cephalopod or clymenia shales". The possible correspondence of this area in SW England is that of the East Ogwell-Lemon Valley area, where a few phacopids were found by Thomas (1909).

*1 Tucker (1976) describes the origins of submarine rises as either from "the volcanic seamounts" or "the reefs". Tucker (1973, 1976), divided this area into three, the North-West basin which received turbidite materials from the Old Red Continent in the North, the mid-geosynclinal rise and the South-East basin which derived greywacke materials from the Mittel Deutsche Schwelle in the South.

Other phacopid-bearing Hercynian Magnafacies can be seen in the areas of Brittany in W France, Harz in Germany, Silesia and the Holy Cross Mountains in Poland, Moravia in Czechoslovakia, the Carnic Alps of Austria and the Urals (?northern Mugodjar) of the U.S.S.R., while the phacopid-bearing Rhenish Magnafacies can be found in Morocco, Portugal, ?Ural Mountains and central Kazakhstan in the U.S.S.R. All these areas are palaeogeographically distributed within the Rhenish-Bohemian and Uralian Seas, and are peripheral or close to the surrounding continents or small islands within these seas.

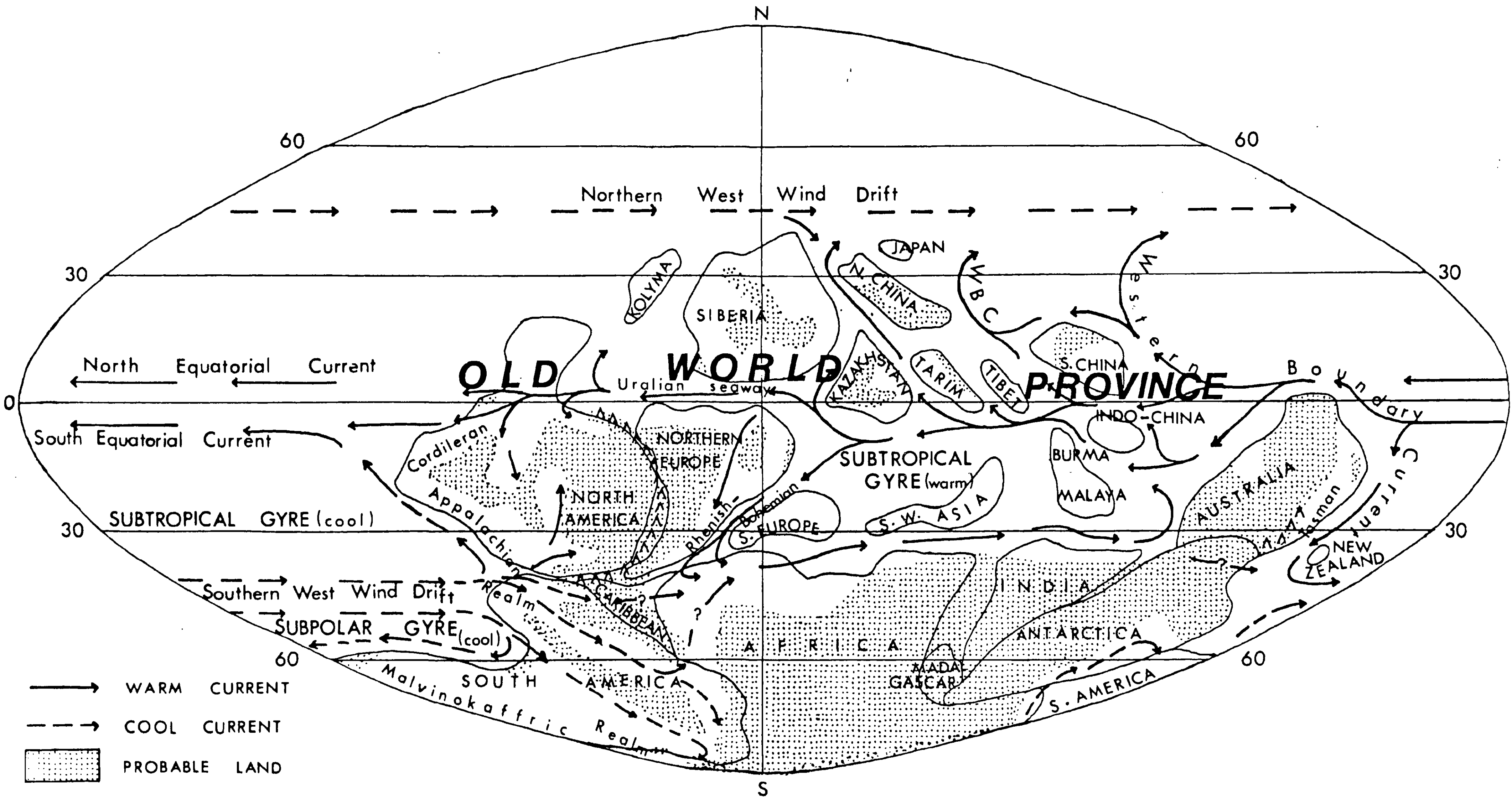
5. 5 General palaeobiogeography of the upper Famennian phacopids

The major occurrences of the Upper Devonian phacopids are reported from the Rhenish-Bohemian subprovince (includes SW England, Belgium, France, Germany, Poland, Austria and Portugal) and the Uralian subprovince (includes the Ural Mountains and northern Mugodjar) by Chlupáč (1977^{i,ii}), Hahn & Hahn (1975) and Maksimova (1980). (see also text-fig. 3.2, p.110f and table 3.4, p.110f). Some minor occurrences are reported from North Africa, Asia Minor, Kazakhstan, SW Asia and China by the same authors, as well as N America (Chlupáč 1977^{ii}) and Vietnam (Hahn & Hahn 1975). All these areas are of tropical to subtropical climate surrounding the ?Palaeotethys Sea (except the N America), where the warm subtropical gyre circulated (Heckel & Witzke 1979). See text-fig. 5.2, p.135f.

Of the six genera entering the Famennian stage, only two (i.e. genus *Phacops* and *Cryphops*) survive to the end of this stage, together with the later derived genus *Dianops*. *Dianops*, which appears in the middle Famennian (*Platyclymenia Stufe*), later becomes the most diverse phacopid genus in the upper Famennian (*Clymenia* and *Wocklumeria Stufen*). This blind genus usually occurs together with the reduced eye phacopids (i.e. genus *Cryphops* and the small eye subspecies of *Ph. wedekindi*) in the Hercynian Magnafacies, although sometimes they are found in the deeper part of the Rhenish Magnafacies, together with the well-developed eye phacopids. The occurrence of so many local species in the genus *Dianops*

⟶

text-figure 5.2



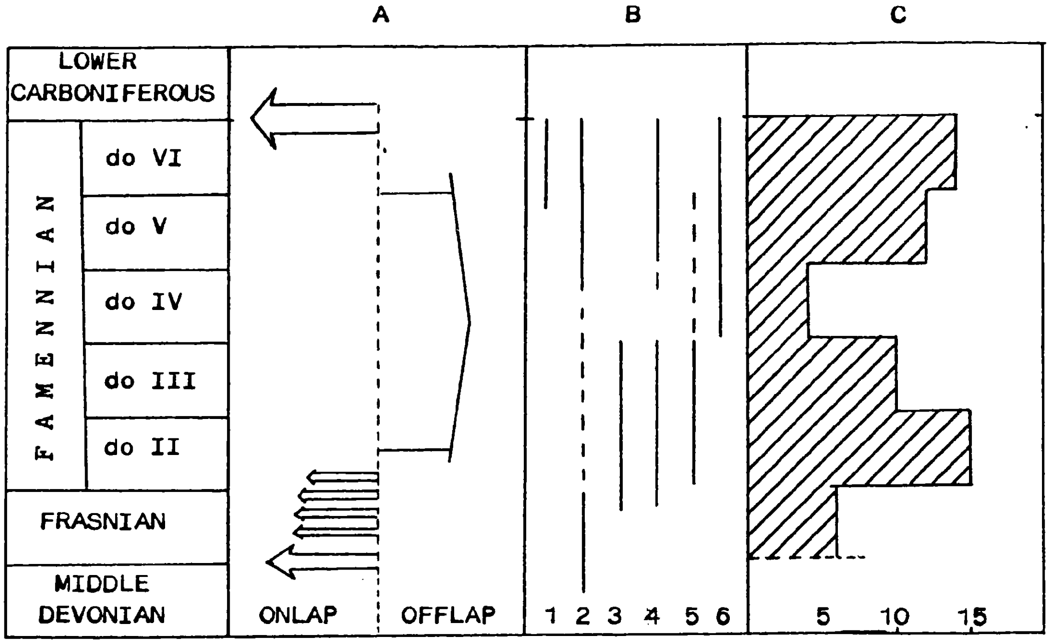
Text-figure 5.2: DEVONIAN WORLD PALAEOGEOGRAPHY AND PALAEOCEANOGRAPHY (after Heckel and Witzke, 1979) (e.g. *D. combensis* and *D. tripartitus* in SW England, *D. bartzschi* in the Thuringia area, *D. typhlops* and *D. trifolius* in Poland, *D. vicarius* in Czechoslovakia and *D. aktjubensis*, *D. pernai* and *D. latilimbatus* in the U.S.S.R.) indicates that most of the species of *Dianops* are restricted to local basins. The occurrence of these blind genera and the reduced eye phacopids in the Ural region is terminated at the end of the *Clymenia Stufe*, and this might indicate the termination of the basinal facies in this subprovince.

The restriction during the following *Wocklumeria Stufe*, however, does not apply to the very well-developed eye phacopids from the subgenus *Phacops* (*Omegops*) which represents the only phacopids outside the Rhenish-Bohemian subprovince. This subgenus which was introduced at the beginning of the *Wocklumeria Stufe*, has its widest spatial range in the latest stage of the Famennian. This subgenus occurs in the shallow water Rhenish Magnafacies in N African and Kazakhstan territory as well as in the Rhenish Mountains, N France/S Belgium and SW England (from N Devon, Launceston, Chudleigh and the study area) areas.

5.6 Upper Devonian phacopid faunas in relation to the change in sea level

The Frasnian transgression which continues into the lower Famennian, widened the basinal areas and led to the origins of the reduced eye phacopids and blind phacopids, to suit the increase in the depth of the water. Early in the middle Famennian the phases changed, a regression extended the shallow Rhenish Magnafacies and restricted the basinal areas. This regression produced the very well-developed eye phacopids in the upper Famennian. In the uppermost Famennian (as shown in the main localities of the study area) the final Devonian transgression took place and that led to the extinction of all phacopid trilobites. A general summary of topics 5. 5 and 5. 6 is given in text-figure 5. 3, below).

Text-figure 5. 3 Relationships between the major sea-level changes and the distribution of the phacopid trilobites (subfamily Phacopinae) during the Upper Devonian



A = Main transgressive and regressive phases in Upper Devonian of Europe (after House 1975^{ii})

B = Stratigraphic ranges of the phacopid genera.

1. Ph. (Omegops)	2. Phacops or Ph. (Phacops)
3. Nephranops	4. Cryphops
5. Trimerocephalus	6. Dianops

C = Distribution of phacopid species during the Upper Devonian (after Osmolska 1963, Pfeiffer 1959 and R. & E. Richter, 1926, 1955)

5. 7 Conclusions

Lack of direct evidence on the foundation of the Rora Slate renders the present author unable to construct a palaeogeographical picture of the study area with absolute certainty. However, indirect evidence from the study area and the surrounding areas does suggest that the palaeogeographical position of the study area might be on a drowned submarine rise (separated from the Chudleigh submarine rise) or, alternatively, on a drowned outer shelf.

In the Upper Devonian of SW England, the study area is included in the "Hercynian" or basinal magnafacies together with the Chudleigh and Newton Abbot areas. The "Rhenish" or shelf magnafacies is situated to the North, while the Old Red Sandstone facies is further North. The palaeogeography of the SW England Upper Devonian is very similar to that of the N European continent, but no close analogue of the study area can be found in N Europe.

The distribution of the Upper Devonian phacopids show a close relationship to the major facies and the change in sea-level, where the well developed eye phacopids spread out during the regression time, while the reduced eye and blind phacopids spread during the transgression time.

CHAPTER 6

CONCLUSIONS

During this research the phacopid faunas of the Rora Slate (Liverton-Ilsington-Bickington area) were studied; classified and described, while the other members of the faunas were identified. The phacopid fauna from the Launceston and Chudleigh areas of SW England and the Rhenish Mountains of Germany were also studied for the purposes of comparison. The importance of the phacopid faunas of the study area in local and Eurasian Upper Devonian stratigraphy, palaeoecology and palaeogeography has become steadily more evident during the progress of this research.

The phacopid faunas are here comprised of 3 genera; *Phacops* (including subgenus *Ph.* (*Omegops*)), *Cryphops* and *Dianops*, with 11 species including *Ph.* (*Om.*) Sp. B, *Ph. granulatus* Münster, *Ph. wedekindi* ssp. A, *Ph. wedekindi occidentalis* n.ssp., *Ph. wedekindi microps* n.ssp., *Cr?wocklumeriae lounstonensis* n.ssp., *Cr? ensae* (R. & E. Richter), *Cr.* sp. A, *D. tripartitus* (Thomas), *D. griffithides griffithides* (R. & E. Richter), *D. limbatus* (Reinh. Richter), *D. combensis* n.sp., and *D.* sp. A.

Among the new discoveries within the studied phacopid fauna are new subspecies *Phacops wedekindi occidentalis*, *Phacops wedekindi microps* and *Cryphops*? *wocklumeriae lounstonensis* and new species *Dianops combensis*. Another interesting aspect is the reassignation of *Dianops tripartitus* from *Cryphops tripartitus* (Thomas) and since this species sometimes possesses a secondary visual surface, a new amended diagnosis of the genus *Dianops* was necessary. Furthermore during this research the present author found several new forms of phacopids including *Phacops wedekindi* ssp. A, *Phacops* (*Omegops*) sp. B, *Cryphops* sp. A and *Dianops* sp. A. Although these new forms differ strongly from other phacopid species or subspecies, the present author cannot assign them with certainty into new species or subspecies because of their small number of occurrences. Also found in the study area are several juveniles of *Phacops wedekindi occidentalis*, *Cryphops*? *wocklumeriae lounstonensis*, and for the first time juveniles of *Dianops griffithides griffithides* and *Dianops tripartitus*. Of similar interest is a new form of transitory pygidium of *Dianops* sp. indet. which has never been recorded before. The mesial tubercle which is projected like a spine on the occipital ring of the *Phacops wedekindi occidentalis* and the functional facial suture in *Cryphops*? *wocklumeriae lounstonensis* and *Dianops tripartitus* are also among other new discoveries in this research. Furthermore the present author also determined dimorphism within *Phacops granulatus* and reclassified Selwood's *Phacops wedekindi* and some of R. & E. Richter's *Phacops wedekindi*.

These phacopid trilobites occur together with proetid trilobites, clymenids, ostracods, corals, brachiopods, bivalves, crinoids and very rarely bryozoans. The index fossils as provided by this assemblage put the Lounston fossil band into the *sphaeroides* subzone (do VI) and the Combe fossil band into the *euryomphala* Zone (do VI). These fossil bands are equivalent to the top of the Mount Pleasant Series of Chudleigh, the Stourscombe Beds of Launceston and the Lower Pilton Beds of North Devon. In continental Europe the equivalent of these fossil bands are the upper "Wocklumer Schichten" and the "Hangenberg

Schiefer" of Rhenish Schiefergebirge and the upper "Clymenia Schichten", upper "Clymenia Kalk" or upper "Cypridinen Schiefer" of the Ostthuringen Schiefergebirge.

Palaeoecologically the Lounston fossil band and Combe fossil band are strongly contrasted. The Lounston fossil band has a very rich fauna with a very high diversity while the Combe fossil band although its fauna is quite rich but has a low diversity. The above differences supported by the differences in the trilobite composition (especially the phacopids) suggest that the Lounston fossil band was deposited on a shallower water environment with richer nutrients compared to the Combe fossil band. Grouping of the sighted phacopids and the blind ones in a local succession in the Lounston fossil band indicate the influence of the late Famennian transgression.

For the palaeoecological study the undisturbed "Salterian moult" which is the most common mode of phacopid ecdysis, was used as the main "biocoenosis" evidence, beside the intact dead trilobites, intact bivalves and brachiopods and coral roots.

Although the study area is geographically very close to the Chudleigh area, palaeogeographically (in the Upper Devonian) they are separated by at least a deep basin which discouraged the migration of some benthic forms (including some phacopids) between these two areas. This exclusion of the study area from the Chudleigh "submarine rise", their faunas and lithologies and evidences (faunas and lithologies) from the shallower marine including the Launceston and North Devon Coast areas, suggests that the study area was deposited on a drowned outer shelf.

From the aspect of the phacopid palaeobiogeography, the phacopid assemblages from the study area, the Chudleigh area, the Launceston area and some others from North Devon, NW Dartmoor and Viverdon Down marked the western boundary of the Eurasian phacopid realm during the uppermost Devonian. Furthermore these assemblages also marked the last Phacopidae since this family became extinct before the Carboniferous Period began. Phylogenetically the distribution of the Upper Devonian phacopids is closely associated with the major change in sea-level (transgression/regression).

APPENDIX I - Chosen measurements for type specimens (In mm)   H = Holotype   P = Paratype

Specimen No.	Species	Type	A	B	C	C'	C_1	D	D_1	I	I_1	I'	J	K	K_1	K_2	∢ glab	P	Q	W	X	Z
Zo 4541	*Ph. wedekindi wedekindi*	H	6.7	5.9	1.8	1.3	1.4	1.8	1.7	11.8	11.8	9.2	6.4	3.2	3.0	6.4	65°	-	-	-	-	-
Zo 4542	" " "	P	5.9	5.1	1.3	0.9	0.9	1.6	1.3	8.0	7.8	6.2	4.8	2.2	2.1	5.0	70°	-	-	-	-	-
Zo 4558	*Ph. wedekindi microps*	PI	5.6	4.8	1.1	-	-	1.4	1.4	9.8	9.8	8.0	6.0	-	-	6.0	70°	-	-	-	-	-
Zo 4559	" " "	PII	6.4	5.5	1.5	-	-	2.3	1.5	-	-	-	-	-	-	-	-	-	-	-	-	-
Zo 4579	*Cr? wocklumeriae lounstonensis*	H	4.2	3.6	-	-	-	1.3	1.2	6.5	6.4	5.6	-	1.9	1.8	4.2	80°	-	-	-	-	-
Zo 4583	" "	P	3.3	2.6	-	-	-	1.1	1.0	5.2	5.0	4.6	-	1.4	1.4	3.5	85°	-	-	-	-	-
Zo 4681	*D. combensis*	H	4.6	3.8	-	-	-	1.0	1.0	7.5	7.5	6.6	-	2.4	2.2	4.7	70°	-	-	-	-	-
Zo 4682	" "	PI	6.5	5.3	-	-	-	1.6	1.6	12.0	12.0	10.6	-	3.8	3.5	6.6	73°	-	-	-	-	-
Zo 4683	" "	PII	5.2	4.4	-	-	-	1.0	1.0	10.4	10.3	8.7	-	3.0	2.8	4.7	60°	-	-	-	-	-
Zo 4684	" "	PIII	7.9	4.5	-	-	-	1.7	1.3	9.0	9.0	7.8	-	3.0	2.9	5.4	65°	17.2	9.3	5.8	1.5	1.9

REFERENCES

ALBERTI, H. 1972. Ontogenie des Phacops accipitrinus. Neues Jahrb. Geol. Paläontol. Abh. 141, 1, 1-36, 6pls.

_____ 1979. Devonian Trilobite Biostratigraphy. In House, M.R., Scrutton, C.T. and Bassett, M.G. (eds). The Devonian System. Spec. Pap. Palaeontol. 23, 313-324.

ALLEN, J.R.L. 1979. Old Red Sandstone facies in external basins, with particular reference to Southern Britain. In House, M.R., Scrutton, C.T. and Bassett, M.G. (eds). The Devonian System. Spec. Pap. Palaeontol. 23, 65-80.

AUSTIN, R.L. et al. 1970. The value of conodonts in the recognition of the Devonian-Carboniferous boundary, with particular reference to Great Britain. Cr. 6e Congr. Int. Strat. Geol. Carbon (Sheffield 1967), 2, 431-444, pl.1.

BREIVEL, M.G. et al. 1967. Devonian of the Eastern Slope of the Urals. In Oswald, H. (ed). Int. Symp. Devonian Syst., Calgary 1967, 1, 421-432.

BRISTOW, C.M. 1963. The Geology of the area between Ilsington, Bickington and Liverton. Proc. Ussher Soc. 1, (2), 65-67.

BURTON, C.J. 1969. Variation studies of some phacopid trilobites of Eurasia and North West Africa, Ph.D. thesis.

_____ and ELDREDGE, N. 1974. Two new subspecies of Phacops rana (Trilobita) from the Middle Devonian of North-West Africa. Palaeontology. London, 17, (2), 349-363, pls. 47-48.

BUTLER, D.E. 1981. Marine faunas from concealed Devonian rocks of Southern England and their reflection of Frasnian transgression. Geol. Mag. 118, (6), 679-697.

CHLUPÁČ, I. 1966. The Upper Devonian and Lower Carboniferous trilobites of the Moravian Karst. *Sb. geol. Ved*, Rada P, *7*, 5-143, pls. 1-24.

——— 1975. The distribution of phacopid trilobites in space and time. *Fossil and Strata*, *4*, 399-408.

——— 1977$^{\text{i}}$. The phacopid trilobites of the Silurian and Devonian of Czechoslovakia. *Rozpr. ustred. Ustavu geol.*, *43*, 1-172, pls. 1-32.

——— $^{\text{ii}}$. The late Devonian and early Carboniferous Trilobite faunas of Moravia. *Symp. Carb. Strat.* (Praha), 305-314.

CLARKSON, E.N.K. 1966. Schizochroal eyes and vision in some phacopid trilobites. *Palaeontology. London*, *9*, (1), 464-487.

——— 1967. Environmental significance of eye reduction in trilobites and recent arthropods, *Mar. Geol.*, *5*, 367-375.

DEARMAN, W.R. and BUTCHER, N.E., 1959. The geology of the Devonian and Carboniferous Rocks of the North-West Border of the Dartmoor Granite, Devonshire, *Proc. Geol. Assoc. London*, *70*, 51-92.

EDMONDS, E.A., McKEOWN, M.C. and WILLIAMS, M. 1975. *South-West England*, Brit. Reg. Geol., 4th ed., H.M.S.O.

ELDREDGE, N. 1971. Allopatric models in Palaeozoic invertebrates. *Evolution*, *25*, (1), 156-167.

ERBEN, H.K. and ZAGORA, K. 1967. Devonian of Germany. *In* Oswald, H. (ed.) *Int. Symp. Devonian Syst., Calgary*, 1967, *1*, 53-68.

GOLDRING, R. 1962. The Bathyal Lull; Upper Devonian and Lower Carboniferous sedimentation in the Variscan geosyncline. *In* Coe, K. (ed.) *Some aspects of the Variscan Fold Belt*, 75-91, Manchester.

_____ 1970. The Stratigraphy about the Devonian-Carboniferous boundary in the Barnstaple area of N. Devon, England. C.r. 6e. Congr. Int. Strat. Geol. Carbon. (Sheffield 1967), 2, 807-816, pl.1.

_____ and LANGENSTRASSEN, F. 1979. Open-shelf and near-shore clastic facies in the Devonian. In House, M.R., Scrutton, C.T. and Bassett, M.G. (eds), The Devonian System. Spec. Pap. Paleontol., 23, 81-97.

_____ et al. 1967. Devonian of Southern Britain. In Oswald, H. (ed.) Int. Symp. Devonian Syst., Calgary 1967, 1, 1-14.

GOODAY, A.J. 1978. The Devonian. pp. 101-120, pls. 1-3. In Bate, R. and Robinson, E. (eds) A stratigraphical index of British Ostracoda. Geol. J. Spec. Issue. Liverpool.

HAHN, G. and HAHN, R. 1975. Die Trilobiten des Ober-Devon, Karbon und Perm. Leitfossilien, 1, 1-127, pls. 1-12.

HARRINGTON, H.J. et al. 1959. In Moore, R.C. (ed.) Treatise on Invertebrate Paleontology, part (O), Arthropoda 1, 560pp., Geol. Soc. Am. Univ. Kansas Press.

HECKEL, P.H. and WITZKE, B.J. 1979. Devonian World Palaeogeography determined from distribution of carbonate and related lithic palaeoclimatic indicators. In House, M.R., Scrutton, C.T. and Bassett, M.G. (eds) The Devonian System. Spec. Pap. Paleontol., 23, 99-123.

HOUSE, M.R. 1963. Devonian ammonoid successions and facies in Devon and Cornwall. Q.J. geol. Soc. London, 119, 1-27, pls. 1-4.

_____ 1975^{i}. Facies and time in Devonian tropical areas. Proc. Yorkshire Geol. Soc. 40, (2), 233-288, pl.19.

_____ 1975^{ii}. Faunas and time in the marine Devonian. ibid., 40, (4), 459-490, pls. 30-31.

_____ 1979. Biostratigraphy of the early ammonoidea. In House, M.R., Scrutton, C.T. and Bassett, M.G. (eds) The Devonian System. Spec. Pap. Palaeontol., 23, 263-280.

_____ and BUTCHER, N.E. 1973. Excavations in the Upper Devonian and Carboniferous rocks near Chudleigh, South Devon. *Trans. R. geol. Soc. Cornwall.* *20*, (3), 199-220, pl. 1.

_____ and SELWOOD, E.B. 1965. Palaeozoic palaeontology in Devon and Cornwall. *In* Hosking, K.F.G. and Shrimpton, G.J. (eds) *Present views of some aspect of the geology of Cornwall and Devon*, 150th anniversary Volume (for 1964). *R. Geol. Soc. Cornwall*, 45-86, 4pls.

_____ *et al.* 1977. *A correlation of Devonian rocks of the British Isles.* *Geol.Soc. London, Spec. Report*, No.7, 110pp.

HUPE, P. 1955. (1953-1955). Classification des Trilobites. *Ann. Paleontol. Paris*, *39*, 59-168 and *41*, 91-325.

KAYSER, F. 1889. Ueber das Devon in Devonshire und im Boulonnais. *Neues Jahrb. Mineral. Geol. Palaontol.*, *1*, 179-191.

KOŚCIELNIAKOWSKA, O. 1967. Upper Devonian in the northern part of the Święty Krzyz (Holy Cross) Mountains. *Biul. geol. Univ. Warsaw*, *8*, 54-118, 10pls.

KREBS, W. 1979. Devonian Basinal Facies. *In* House, M.R., Scrutton, C.T. and Bassett, M.G. (eds) *The Devonian System.* *Spec. Pap. Palaeontol.* *23*, 125-139.

MAKSIMOVA, Z.A. 1955. Trilobity srednego i verchnego Urala i severnych Mugodshar. *Trudy vsesojusn. nautschno-issled. geol. Inst. (VSEGEI), n.s.*, *3*, 1-263.

_____ 1980. Biostratigraphic zones based on trilobites in U.S.S.R. Devonian deposits. *Int. geol. Rev.*, *22*, (4), 477-489.

MOORE, R.C. 1959. (ed.) *Treatise on invertebrate paleontology, Part O, Arthropoda I*, 560pp. *Geol. Soc. Am.*, Univ. Kansas Press.

OSMOLSKA, H. 1958: Famennian Phacopidae from Holy Cross Mountains (Poland). *Acta Pal. Pol.*, *3*, (2), 119-148, Pls. 1-4.

______ 1963. On some Famennian Phacopinae (Trilobita) from Holy Cross Mountains (Poland). *Acta Pal. Pol.*, *8*, (4), 495-523, pls. 1-4.

PAECKELMANN, W. (1913). Das Oberdevon des Bergischen Landes., *Abh. preuß. geol. L.-A*, *70*, 1-356, pls. 1-7.

PAPROTH, E. and STREEL, M. 1970. Correlations biostratigraphiques pres de la limite Devonian/Carbonifere entre les facies littoraux ardennais et les facies bathyaux rhenans. *Coll. sur la Strat. du Carbon.* (Sheffield 1969), *555*, 365-368, pls. 24-26.

PFEIFFER, H. 1954. Der Bohlen bei Saalfeld/Thuringen. *Beih. Geol.* *11*, 1-105, pls. 1-9.

______ 1959. Neue Beobachtungen und Funde aus dem Saalfelder Oberdevon. *Geologie DDR*, *8*, (3), 262-272, pls. 1-4.

REID, C. *et al.* 1911. The geology of the country around Tavistock and Launceston. *Mem. Geol. Surv. G.B.*

RICHTER, R. and RICHTER, E. 1926. Die Trilobiten des Oberdevons. Beitrage zur Kenntnis devonischer Trilobiten IV. *Abh. preuß . geol. L.-A.*, *99*, 1-314, pls. 1-12.

______ 1928. Trilobitae neodevonici. *Fossilium Catalogus 1, Animalia*, *37*, 1-160, 9 pls.

______ 1933. Die letzen Phacopidae. *Bull. Mus. roy. Hist. natur. Belg.*, *9*, 1-19, pls. 1-2.

______ 1955. Oberdevonische Trilobiten, Nachtrage. 1 - Trilobiten aus der *Prolobites*-Stufe III. 11 - Phylogenie der Oberdevonischen Phacopidae, *Senckenbergiana Lethaea*, *36*, 49-72, pls. 1-2.

ROEMER, F. 1880. Notice of the occurrence of Upper Devonian Goniatite Limestone in Devonshire. Geol. Mag., 7, (4), 145-147.

RZHONSNITSKAYA, M.A. 1967. Devonian of the U.S.S.R. In Oswald, D.H. (ed.), Int. Symp. Devonian Syst., Calgary 1967, 1, 331-348.

SALTER, J.W. 1864. A Monograph of British trilobites. Palaeontogr. Soc. Monograph, 16, 1-83.

SCHINDEWOLF, O.H. 1937. Zur Stratigraphie und Pälaontologie de Wocklumer Schichten (Oberdevon). Abh. preuß. geol. L.-A., 178, 1-132.

SELWOOD, B.E. 1959. The Upper Devonian and Carboniferous geology of the Launceston area of Cornwall. Ph.D. thesis.

——— 1960. Ammonoids and trilobites from the Upper Devonian and lowest Carboniferous of the Launceston Area of Cornwall. Palaeontology. London, 3, (2), 153-185, pls. 26-29.

——— and BURTON, C.J. 1969. Possible dimorphism in certain Devonian phacopids (Trilobita). Int. Un. Geol.Sci. A, 1, In Westermann, G.E.G. (ed.) Sexual dimorphism in fossil Metazoa and taxonomic implications., 196-200.

——— In House, M.R. et al (eds) 1977. (see House)

——— et al in ibid.

STRUVE, W. In Moore, R.C. (ed.) 1959. (see Moore).

——— 1976. Beitrage zur Kenntnis der Phacopina (Trilobita), 9 - Phacops (Omegops) n.sg. (Trilobita: Oberdevon). Senckenbergiana Lethaea, 53, (6), 429-451.

STUBBLEFIELD, C.J. 1936. Cephalic structures and their bearing on current classification of trilobites. Biol.Review. 11, 407-440.

THOMAS, I. 1909. Notes on Trilobite Fauna of Devon and Cornwall. *Geol. Mag.*, *46*, 193-204.

TUCKER, M.E. 1973. Sedimentology and diagenesis of Devonian pelagic limestone (Cephalopodenkalk) and associated sediments of the Rhenohercynian Geosyncline, West Germany. *Neues Jahrb. Geol. Paläontol.* Abh. *142*, 320-350.

______ 1974. Pelagic Sediments on Land and under the Sea. *In* Hsu, K.J. and Jenkyns, H.C. (eds). *Spec. Publ. Int. Assoc. Sedimentol.*, *1*, 71-92.

USSHER, U.A.E. 1890. The Devonian rocks of South Devon. *Q.J. Geol. Soc. London*, 46, 487-517.

______ *et al.* 1913. The geology of the country around Newton Abbot. *Mem. Geol. Surv. G.B.*

WATERS, R.A. 1970. The Variscan structure of eastern Dartmoor. *Proc. Ussher Soc.*, *2*, 191-197.

WEDEKIND, R. 1914. Monographie der Clymenien des Rheinischen Schiefergebirge. *Abh. Ges. Wiss. Gottingen. Math.-phys. Kl.*, *10*, 1-73, 7 pls.

WEYER, D. 1975. Biostratigraphy of the Devonian-Carboniferous boundary in the German Democratic Republic. (Abstract of papers) in *VIII Int. Congr. Carbon. Strat. Geol. Moscow* 1975, 299-300.

WHITELEY, M.J. 1981. The faunas of the Viverdon-Down area South-east Cornwall. *Proc. Ussher Soc.*, *5*, 186-193, pl. 1.

ZIEGLER, P.A. 1980. *Geological Atlas of Western and Central Europe.* Shell Int. Petroleum B.U., The Hague, The Netherlands.

ZIEGLER, W. 1971. Conodont stratigraphy of the European Devonian. *Mem. Geol. Soc. Am.*, *127*, 227-284.