BLINDING AND EXTINCTION OF CERTAIN PROETIDAE (TRIL.)

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ABSTRACT—Eye reduction and subsequent blindness of Devonian Proetinae and Tropidocoryphinae increase in the Upper Devonian and Lower Carboniferous. These phenomena result from two different phyletic modes : the "*Waribole*—mode" and the "*Piriproetus*—mode", both characterized by specific changes in the course of the facial suture. Aberrant courses of the suture are extreme modifications of these modes. The rates of reduction of the palpebral lobe and of the visual surface are not strictly co-ordinated, but related in a rather general manner.

The ecologic and phylogenetic significance of blinding of the Proetinae is discussed. It occurred mostly, but not exclusively, in European regions. This eye reduction is a reversive tendency the origin of which seems to be accidental and pre-adaptive, i.e., independent of environment. Later, after immigration into an adequate environment which is considered to be represented by the offshore facies, and during the Upper Devonian expansion of this facies, eye reduction became a tendency of positive selective value which advanced orthogenetically.

By the approach of larger orogenies of late Lower and of Upper Carboniferous time, the adequate environment in the Hercynian geosyncline tended to disappear, and the Proetinae became extinct. This extinction, however, is not considered to be caused by the tectonic events, for environments similar to the original one remained available. The extinction of the Proetinae is interpreted as a result of selection (disappearance of original environment) and apparent inability for producing novel adaptive tendencies which would have enabled the populations to move into other remaining environments. This signifies that the eye reduction during the preceding phyletic development had become an overspecialisation and therefore a typolytic feature.

The typolysis of the Proetinae is connected with numerous "atavistic" and some aberrant features, all of them related to the eye and to the facial suture which depends on the eye.

Some phylogenetical phenomena are discussed.

INTRODUCTION

THE author has studied the relationship between blinding and facial sutures in Devonian and Lower Carboniferous Proetinae and Tropidocoryphinae. In the following pages, however, only the general features of the results are presented ; taxonomic details and descriptions of new species with reduced eyes will be given in a future paper.
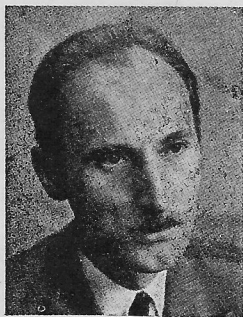
It is a well-known and conspicuous fact that during Upper Devonian and Lower Carboniferous time a considerable number of phacopid and proetid species became blind or were subjected to a reduction of the visual organs. Although in the Upper Devonian other trilobite families are represented only scarcely, R. & E. Richter (1926: 9) mention that within the 32 described species of Phacopinae and Dalmanitinae with known visual region, 9 are blind. Completing further the information given by these authors, it should be reported that within the 54 (+2) Upper Devonian species of the Proetinae and Tropidocoryphinae (*sensu* Pribyl 1946a) with known ocular region, 44 show eye reduction. In the Lower Carboniferous both subfamilies are represented by 36 (+3) forms with known eye region, 35 of them showing reductions of the visual organ.

This tendency of eye reduction (blinding) in the above-mentioned sub-families apparently reached its climax during Lower Carboniferous time and was very frequent in the Upper Devonian (Text fig. 5). Recently, however, blind proetids have also been reported from the Lower and Middle Devonian (Ruzicka 1946 ; Pribyl 1946a ; Pribyl & Plas 1954), as well as other proetids with reduced eyes (Erben 1952 ; Pillet 1952). Besides, Reinh. Richter (1863) and R. & E. Richter (1943) had described two Middle Devonian species with eye reduction, which, however, remained imperfectly known. It seems that some of the mentioned Lower Devonian species have to be considered as the phylogenetic ancestors of certain Upper Devonian groups (*Piriproetus* Erben 1952 ; but not *Eodrevermannia* Pribyl 1946).

In Ordovician proetids, eye reduction also does occur although apparently no case of blindness is known. However, due to the fact that the taxonomy of the Ordovician proetids is still problematical, this group is not dealt with in the present paper.

"Visual organ" or "eye" or "eye region" is used for the unit which consists of the palpebral lobe and the visual area, i.e., the facet-bearing part. In speaking of "blind" species or of "blindness", the writer refers to the complete lack of facets, because in these cases, we can presume that the eye probably had ceased to be functional. The preceding phylogenetical processes, i.e., the rudimentation of palpebral lobe and visual area, which leads to blindness, are referred to under the term "reduction of the eye". The turning points a, β, γ, etc., of the facial suture are explained in text-fig. 1. The term "exsag." is used for directions which are sub-parallel to the axis (=exsagittal), and "transv." is used for directions transverse to it. The frequently used letters "R. R." and "R. & E. R." substitute the names of Rudolf Richter and Rudolf & Emma Richter.

The writer wishes to express his gratitude to Professor C. Kockel for the loan of blind proetids ; to Dr. K. Sdzuy for information concerning the suture of *Carbo-*

1. EVOLUTION OF FACIAL SUTURES DURING EYE REDUCTION

The "normal" eye in the Proetidae is situated in the posterior part of the cephalon, occupying approximately a portion (exsag.) of the free cheek which in length corresponds to the space between the posterior border furrow and ± mid-length of the glabella. In this stage (I), the posterior branch of the facial suture is short, the turning points ϵ and ξ are nearly joined, and w is relatively close to the axial furrow. During the following reduction, in all cases the palpebral lobe successively becomes shorter (exsag.) while the anterior tip of the palpebral lobe and the visual area remains in its former position. Thus shortening affects the posterior parts of the palpebral lobe, which is also indicated by an increase in the length of the posterior branch of the suture and by a separation of ϵ from ξ. This early stage (II) in the reduction in size of the palpebral lobe (and often of the whole of the eye) has been incorrectly called "shifting forward". ("Vorruecken"—R. & E. R. 1951 : 226).

Although this early phase is common to all instances of eye reduction in proetids, it manifests itself in two different patterns in the course of the posterior branch of the suture. In one of the two resulting morphological stages the eye reduction terminates. The other gives rise to further reduction, characterized by specific changes in the course of the suture, which result in a specific sequence of morphologic stages. Briefly, the writer will refer to the two different modes as "*Waribole*-mode" and "*Piriproetus*-mode". In spite of their aberrant aspect, to these two modes some other developments of suture can be related.

R. R. (1932 : fig. 3) presented a "*Pteroparia—Reihe*" and a "*Drevermannia—Reihe*" as tendencies in the blinding of the Upper Devonian proetids, but both do not differ fundamentally and both belong to the "*Piriproetus*-mode" (with regard to *Pteroparia*, see p. 13).
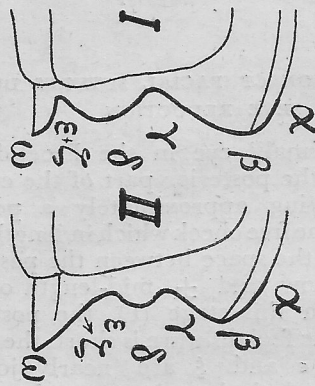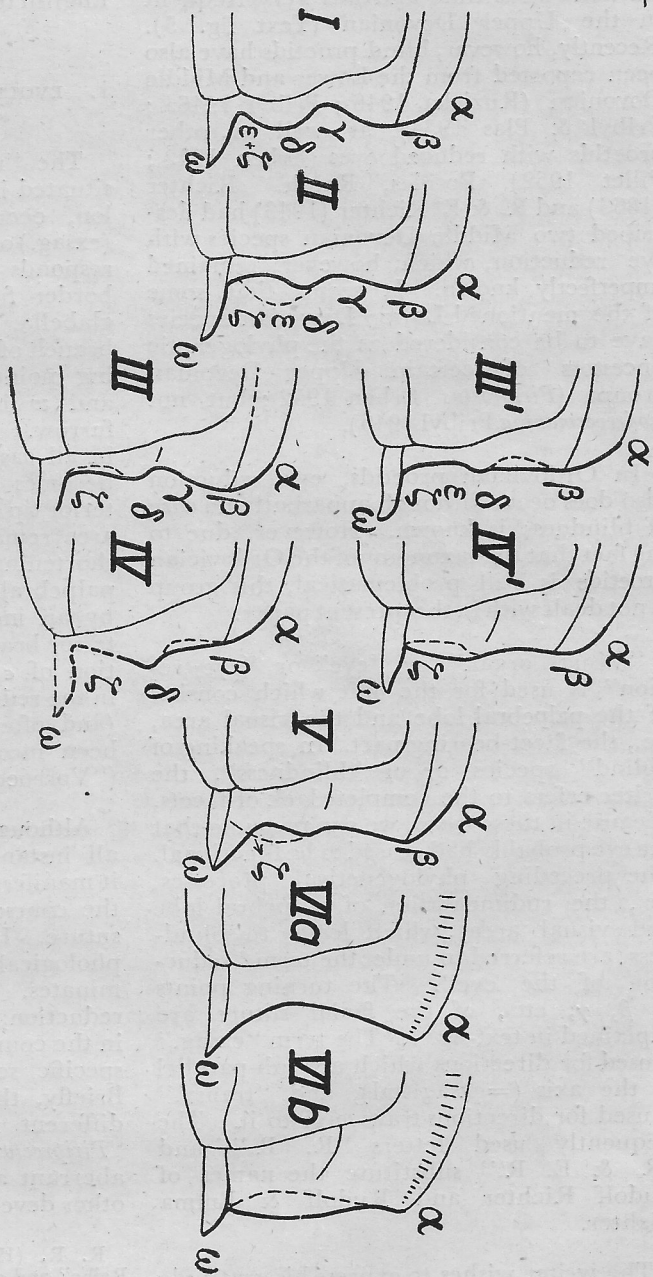
TEXT-Fig. 1

1a. THE WARIBOLE-MODE

The most characteristic features of the *Waribole*-mode are that ξ as an angle disappears already in the earliest phases of eye reduction (by stretching of the posterior branch of the suture), and that in the same stage, γ and ϵ remain close to the axial furrow, the fixed cheek remaining very narrow (transv.) in this part.

The stages of eye obsolescence and suture development in the *Waribole*-mode are (Text-fig. 1) :

Stage I :
Palpebral lobe and visual area "normal", as is also the suture.

Stage II :
Palpebral lobe and visual area shortened, distant from posterior border furrow. ϵ separated from ξ and shifted forward. ξ as an angle has disappeared. γ and ϵ close to axial furrow.

Portion of the fixed cheeks between palpebral lobe and axial furrow is narrow. Stretched posterior branch of suture runs diagonally in a straight line from ϵ to ω, which has been shifted outward laterally.

The best example for the *Waribole*-mode is represented by *Cyrtosymbole* (*Waribole*) R. & E. R. 1926. All the corresponding species from Eifelian ? (? *superstes* Barrande-see Pribyl 1949 : 308) and late Upper Devonian to early Lower Carboniferous belong to stage I. In the late Lower Carboniferous occurs the reduction to stage II (*aequalis* v. Meyer), while a transitional phase can be observed in *laevicauda* Sarres (see text-figs. 1 and 3).

The *Waribole*-mode has been observed in the following genera : *Unguliproetus* Erben 1951 (stages I-II)[1]; *Cyrtosymbole* (*Waribole*) R. & E. R. 1926.

EXPLANATION OF FIGURES

TEXT-FIG. 1—Stages of the facial suture during eye reduction of the Proetidae. Species represented by slightly simplified cranidia only the right side of which is reproduced. In each species, an interrupted line demonstrates the differing part of the suture of the immediate ancestor. Reconstructions of unknown parts of the cranidium are indicated by additional interrupted lines. Sizes slightly generalized.

Piriproetus-mode :

I : *Cornuproetus* (*Cornuproetus*) *neocorrugatus* Erben 1952
II : *Cornuproetus* (*Piriproetus*) *pirus* (Erben 1952)
III : *Cornuproetus* (*Piriproetus*) n. sp. *B*
IV : *Cornuproetus* (*Piriproetus*) n. sp. *C* ["aff. *amblyops*"]
V : *Palpebralia palpebralis* R. & E. R. 1926
VIa : *Palpebralia brecciae* R. R. 1913
VIb : *Palpebralia nodannulata* R. R. 1913
[III' : *Cornuproetus* (*Piriproetus*) *amblyops* (Erben 1952)]
[IV' : *Cornuproetus* (*Piriproetus*) *herrmanni* (R. & E. R. 1943)]

Waribole-mode :

I : *Cyrtosymbole* (*Waribole*), typical development
II : *Cyrtosymbole* (*Waribole*) *aequalis* (v. Meyer 1831)

(α, β, γ, δ, ϵ, ξ, ω : Turning points of the suture ; after Barrande 1852 and R. & E. R. 1940, 1949 ; completed.)

(I—II—III'—IV'—V—VI : Principal representatives of the main *Piriproetus-Palpebralia* branch ; III—IV : accessory branch.)

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[1]Here promoted to generic rank. For genotype and diagnosis see Erben (1951 : 14 ; 1952 : 216). Although probably derived from *Proetus* (*Proetus*) Steininger 1831, *Unguliproetus* shows too strong morphological differences to remain within the genus *Proetus*—For the same reason, the writer accepts J. Pillet's separation (1952) of *Cornuproetus* R. & E. R. 1919 and *Eremiproetus* R. & E. R. 1919 as independent genera. *Xiphogonium* Corda 1847 differs so little from *Cornuproetus* that it must be regarded as a subgenus of this genus instead of *Proetus*. The generic concept of *Proetus* should be restricted to forms without a preglabellar field, and with narrow and shallow anterior border furrow, uniformly convex axial furrows on the glabella, and broad (transv.) pygidial axis. For instance, *Proetus* (*Proetus*) Stein, *Proetus* (*Crassiproetus*) Stumm 1953, and also various Ordovician and Silurian proetids which in general correspond to this type, but probably represent new genera.

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The *Waribole*-mode is present also in the Silurian *Sharyia* Pribyl 1946 (stage II, but modified), which was tentatively referred to the Tropidocoryphinae by its author. It occurs also in the Ordovician *Isbergia* Warburg 1925 .(*planifrons* : /II ; *pervula* (II) which was supposed to belong to the Proetinae by Pribyl (1946a : 4, 5). The Ordovician *Holotrachelus* Linnarsson 1870 also shows the *Waribole*-mode (II), but it could be that the Holotrachelidae are not true Proetoidae as was supposed by Hupe (1953).

In the *Waribole*-mode, the reduction of the eye does not appear to pass beyond stage II, at least not in Devonian and Lower Carboniferous Proetidae. Therefore, no blind species have been found whose eye reduction had followed this mode.

Stage II of the *Waribole*-mode (but γ and ϵ more distant from the axial furrow) is indicated also in the suture of the Otarionidae. Moreover, it resembles very much the type of suture which is typical in numerous Cambrian and Ordovician trilobites (p.e. : many Redlichioidae, Asaphiscoidae, Asaphoidae, Dikelocephaloidae, Ptychoparioidae, Solenopleurioidae, Olenoidae—*sensu* Hupe 1953). Therefore, it has a distinctly archaic aspect.

[The so called "Kambrische Tracht" or "Peltura-Tracht" which R. & E. R. (1949 : 72) observed in the Lower Carboniferous genus *Liobole*, is not identical with stage II of the *Waribole*-mode because it occurs in late stages of eye reduction instead of early ones. As the phylogenetic development of *Liobole* clearly shows, this is a part of the late stages of the *Piriproetus*-mode.]

1b. THE PIRIPROETUS-MODE

This mode of eye reduction and sequence of sutural changes takes its name from *Cornuproetus* (*Piriproetus*) (Erben 1952) where all stages (including the important stage II) of this mode are perfectly developed. This evolutionary tendency is characterized by the fact that in the suture the turning point ξ as an angle does not disappear in early phases (as in the *Waribole*-mode), but in later ones. Moreover, the palpebral lobe tends to vanish completely or to become rudimentary, γ and ϵ becoming obsolete, while both branches of the suture tend to be stretched. Generally, a broadening (transv.) of the fixed cheeks occurs in greater or less degree.

Some of the late stages resemble stage II of the *Waribole*-mode because ξ ceases to be an angle when the posterior branch of the suture stretches. These stages (V or VIa), however, can easily be identified once the phylogeny of the proetid group in question has been investigated and the preceding stages are found to have belonged to the *Piriproetus*-mode, preserving a present ξ in form of an angle or an angular curve. Other criteria for distinguishing this simulated *Waribole*-mode of the late stages are the distance of γ and ϵ (transv. ; broadening of fixed cheek) from the axial furrow and sometimes also the complete lack of the palpebral lobe.

The stages of eye obsolescence and suture development in the *Piriproetus*-mode are (see text-fig. 1) :

Stage I :
  Palpebral lobe and visual area 'normal', as well as the suture.

Stage II :
  Palpebral lobe (and generally also the visual area) shortened, distant from posterior border furrow. ϵ separated from ξ and shifted forward. ξ as an angle well preserved, close to posterior border furrow. γ and ϵ near the axial furrow. ϵ-ξ runs subparallel to axial furrow and close to it. (The angle in ξ sometimes may be slightly rounded. Nevertheless, in ξ constantly remains a distinctly angular curve.)

Stage III :
  ϵ as an angle obsolete or completely disappeared, because posterior branch of suture stretches between δ and still angular ξ. Thus only the anterior border of palpebral lobe is distinct.

[Exceptional stage III' :
  Analogous to stage III but instead of ϵ, γ becomes obsolete and anterior branch stretches first. Thus only the posterior border of palpebral lobe is distinct.]

Stage IV :
  γ as an angle obsolete or completely disappeared, because anterior branch of suture (between δ and β) stretches also. Thus palpebral lobe becomes rudimentary or disappears completely. ξ maintains its former position and shape.

[Exceptional stage IV':

Analogous to stage IV but instead of γ, ϵ becomes obsolete and posterior branch of suture stretches between δ and still angular ξ. Morphologic aspect is thus about the same as in stage IV.]

Stage V :

ξ disappears because the portion of posterior branch which forms its angle becomes stretched (feature similar to *Waribole*-mode). Transitional stages have been observed where ξ occupies an intermediate position.

[In *Palpebralia*, a slight indicated pseudo-palpebral lobe temporarily appears, but it is not homologous to the true lobe (which has disappeared). This homoeomorphous secondary pattern is caused by the still incomplete stretching of the posterior branch. In other genera the rudiment of a true palpebral lobe may remain preserved, as in stage IV. In these genera, during the reduction of the type described above, γ and ϵ became obsolete but did not disappear completely.]

Stage VI :

Further stretching of the entire suture between β and ω. Between these two points, the suture can remain slightly concave toward the free cheek : stage VIa [p.e. : some *Palpebralia*, some *Drevermannia*. *Cyrtosymbole* (*Calybole*), ? *Liobolina*. *Liobole*. *Cystispina*. *Typhloproetus*]. In other cases, it can become almost completely rectilinear : stage VIb [p.e. : some *Palpebralia*, some *Drevermannia*].

The *Piriproetus*-mode is the most common type of eye reduction in the younger Proetidae, and it appears to occur exclusively in this family. In some of these proetid branches, however, the evolution seems to stop before reaching the final stages of eye reduction. Almost always the *Piriproetus*-mode passes through stages III and IV, i.e., the stretching of the suture begins first in the posterior branch. The only exception was observed in the *Piriproetus-Palpebralia* branch (III', IV').

Although the principal structure and sequence of the stages I—VI is common to all cases, in some of the proetid groups it can be accompanied by additional special features :

Rudiments of the palpebral lobe can remain to late stages, even to VIa [*Liobole*, *Liobolina*, *Cyrtosymbole* (*Calybole*)]. On the other hand, the suture may be stretched to stage VIa and the palpebral lobe can disappear completely, but the rudiment of a visual area (on cheek level only, not more elevated) in one species remains [*Typhloproetus schindewolfi*]. Generally, after stage III, the fixed cheek broadens considerably. In some groups, however, the broadening is only moderate or slight [*Typhloproetus*, *Pteroparia*, *Diacoryphe*, ? *Liobolina*]. In some cases, indicated eye ridges reappear, which cause an "atavistic" aspect. In *Liobole* there is a tendency of the rudimentary palpebral lobe to migrate forward. This is a true migration which is not identical with the shortening described on p. 83.

Excellent examples of the *Piriproetus*-mode are the different species of *Liobole*. The common stages III and IV and the exceptional stages III' and IV' occur in two different trends of *Cornuproetus* (*Piriproetus*) (see text-fig. 1).

Within the younger Proetidae and Tropidocoryphinae, the *Piriproetus*-mode has been observed in the following genera : Proetinae :

Proetus (*Proetus*) Steininger 1831 [I-II][1] ; *Proetus* (*Crassiproetus*) Stumm 1953 [I-II] ; *Cornuproetus* (*Piriproetus*) (Erben 1952) [I/II, II, III', IV', III, IV][2] ; *Palpebralia* R. & E. R. 1927 [V, VIa, VIb][3] ; *Dreverman-*

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[1] Z. Kielan (1954) objected to the subdivision of *Proetus* (*Proetus*) in different groups distinguished by the size of the eyes, etc., because they are artificial rather than phylogenetical units. After previous doubts, the writer now accepts her view.

[2] J. Pillet (1952) referred *Piriproetus* to *Cornuproetus* instead of *Proetus*.

[3] *Palpebralia* must be separated as an independent genus from the probably polyphyletic *Drevermannia* because in *Piriproetus* it has its own independent ancestor. The species *herrmanni* R. & E. R. 1943 turned out to belong to *Piriproetus*.

nia (*Drevermannia*) R. R. 1913 [VIa, VIb] ; *Drevermannia* (*Formonia*) R. & E. R. 1927 [VIb] ; *Eodrevermannia* Pribyl 1946 [VIb][1] ; *Chaunoproetus* R. & E. R. 1926 [III ? VIa][2] ; *Perliproetus* R. & E. R. 1926 [II]; *Cyrtosymbole* (*Cyrtosymbole*) R. R. 1913 [I, III] ; *bergica*-group of "*Cyrtosymbole* (*Waribole*)" [III] *Cyrtosymbole* (*Calybole*) R. & E. R. 1926 (II, III, V, VIa] ; *Cyrtosymbole* (*Cyrtodechenella*) R. & E. R. 1950 [I, II] ; *Cyrtosymbole* (*Macrobole*) R. & E. R. 1951 [I, II, ? III ; —*duodecimae* ?] ; *Liobolina* R. & E. R. 1951 [II, ? V] ; *Liobole* R. & E. R. 1949 [II, III, V, VIa] ; *Phillibole* R. & E. R. 1937 [II, III] ; *Cystispina* R. & E. R. 1939 [? III, VIa] ; *Typhloproetus* R. R. 1913 [? IV, VIa] *Skemmatocare* R. & E. R. 1927 [VIa].

Tropidocoryphinae :

  Denemarkia Pribyl 1946 [II] ; *Pteroparia* R. R. 1913 [IV] ; *Carbonocoryphe* R. & E. R. 1950 [II] ; *Diacoryphe* R. & E. R. 1951 [III, IV].

[In the Phillipsiinae and Dechenellinae (both *sensu* Pribyl 1946) a slight eye reduction occurs also, but it is more a reduction of the palpebral lobe than of the entire eye. Equivalents of the *Waribole*-mode and the *Piriproetus*-mode seem to be present in both sub-families, the latter, however, linked with additional evolutionary tendencies, in the Phillipsiinae.]

The tendency represented by the *Piriproetus*-mode appears also in the Ordovician species "*Proetus*" *girvanensis* Nich. & Eth. [II] which according to J. L. Begg (1939 : 373) includes "*Proetus*" *procerus* Nich. & Eth. [3]).

1c.   ABERRANT SUTURES

Within the Proetidae, aberrant sutures occur in *Scharyia* Pribyl 1946, *Skemmatocare* R. & E. R. 1927 and *Pteroparia* R. R. 1913. In *Scharyia*, ω is shifted considerably outward laterally and the posterior branch of the suture runs sigmoidally subparallel to the posterior border furrow (Text-fig. 2f). Although the resulting aspect is most unusual, it is only a slight modification of stage II of the *Waribole*-mode.

EXPLANATION OF FIGURES

TEXT-FIG. 2—Homoeomorphies and "atavistic" features in the facial suture of the younger Proetidae and older trilobites. Simplified cranidia, only the right side of which is reproduced. Sizes generalized.

    a-e : Bending of the anterior branch into oblique backward direction.

    f-g : Shifting outward laterally of ω.

    h-k : Lack of angular turning point ξ in the posterior branch.

      (a) *Amechilus palaora* Ross (Amechilidae—L. Ordovician).

      (b) *Hypothetica rawi* Ross (Amechilidae—L. Ordovician).

      (c) *Entomaspis radiatus* Ulrich (Entomaspidae—U. Cambrian).

      (d) *Skemmatocare elegans* (v. Muenster) (Proetinae—U. Devonian).

      (e) *Pteroparia columbella* R. R. (Tropidocoryphinae—U. Devonian).

      (f) *Scharyia micropyga* (Hawle & Corda) (Tropidocoryphinae ?—Silurian).

      (g) *Cedaria prolifica* Walcott (Cedariidae—U. Cambrian).

      (h) *Cyrtosymbole* (*Waribole*) *aequalis* (v. Meyer) (Proetinae—L. Carboniferous).

      (i) *Olenus*, typical development (Oleninae—U. Cambrian).

(After Rasetti 1952, Hupe 1953, Pribyl 1946, R. & E. R. 1926, 1927, 1937.)

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[1] The blind *Eodrevermannia* exhibits the last stage of eye reduction (VI). Therefore, it would be difficult to consider it as ancestor of the Upper Devonian Drevermannias. Most probably it represents a late or final member of a still undiscovered Lower Devonian branch of Proetidae and, therefore, an independent genus.

[2] As Pfeiffer (1954) pointed out, *Drevermannia* (*Carncia*) R. & E. R. 1927 belongs in synonymy with *Chaunoproetus*.

[3] An examination of specimens from Girvan showed that *girvanensis* does not belong to *Proetus* Stein. This species represents a new genus which resembles closely the genus *Cornuproetus* R. & E. R. 1919, but differs from it in the shape of the hypostome and in the smaller eye which is in stage II of the *Piriproetus*-mode. The new genus differs from *Proetus* (*Proetus*) in its sigmoidal curved axial furrows in the glabellar region [thus resembling *Cornuproetus* (*Cornuproetus*)] in the shape of the pygidium (dto) and in its hypostome.
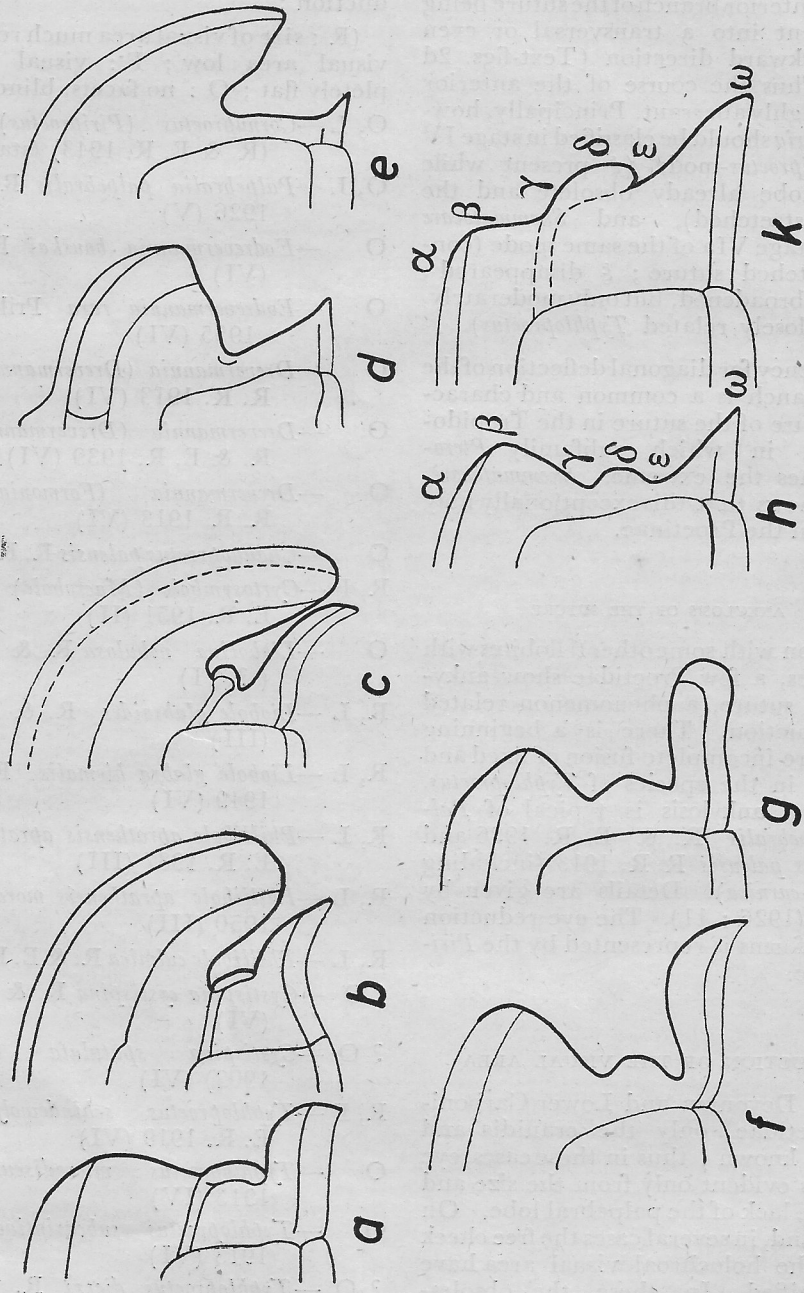
Text-Fig. 2

In *Pteroparia* and *Skemmatocare*, the fixed cheeks between "γ" and β have increased in size, the anterior branch of the suture being strongly bent into a transversal or even oblique-backward direction (Text-figs. 2d and 2e). Thus the course of the anterior branch is highly aberrant. Principally, however, *Pteroparia* should be classified in stage IV of the *Piriproetus*-mode (ξ present while palpebral lobe already obsolete and the branches stretched), and *Skemmatocare* belongs to stage VIa of the same mode (concavely stretched suture ; ξ disappeared ; fixed cheek broadened, but only moderately, as in the closely related *Typhloproetus*).

The tendency for diagonal deflection of the anterior branch is a common and characteristic feature of the suture in the Tropidocoryphinae, in which subfamily *Pteroparia* reaches the extreme. *Skemmatocare*, however, shows that this exceptionally may occur also in the Proetinae.

1d. ANKYLOSIS OF THE SUTURE

In common with some other trilobites with reduced eyes, a few Proetidae show ankylosis of the suture, a phenomenon related to eye reduction. There is a beginning and therefore incomplete fusion of fixed and free cheeks in the species of *Typhloproetus*. Furthermore, ankylosis is typical of *Palpebralia palpebralis* R. & E. R. 1926 and *Chaunoproetus palensis* R. R. 1913 (including "*Carnicia*" *carnica*). Details are given by R. & E. R. (1926 : 11). The eye reduction of all these forms is represented by the *Piriproetus*-mode.

2. REDUCTION OF THE VISUAL AREA

In many Devonian and Lower Carboniferous Proetidae, only the cranidia and pygidia are known ; thus in these cases, eye reduction is evident only from the size and shape or the lack of the palpebral lobe. On the other hand, in several cases the free cheek including the holochroal visual area have been identified. In these the obsolescence of the facets can be readily observed.

The visual area is known in the following species with middle or late stages of eye reduction :

(R. : size of visual area much reduced ; L : visual area low ; F : visual area completely flat ; O : no facets, blind.)

O, L —*Cornuproetus* (*Piriproetus*) *herrmanni* (R. & E. R. 1943) (stage IV')[9]

O, L —*Palpebralia palpebralis* R. & E. R. 1926 (V)

O　—*Eodrevermannia . bouskai* Pribyl 1946 (VI)

O　—*Eodrevermannia rara* Pribyl & Plas 1955 (VI)

O　—*Drevermannia* (*Drevermannia*) *schmidti* R. R. 1913 (VI)

O　—*Drevermannia* (*Drevermannia*) *pruvosti* R. & E. R. 1939 (VI)

O　—*Drevermannia* (*Formonia*) *formosa* R. R. 1913 (VI)

O　—*Chaunoproetus palensis* R. R. 1913 (VI)

R, F —*Cyrtosymbole* (*Macrobole*) *blax* R. & E. R. 1951 (II)

O　—*Liobolina nebulosa* R. & E. R. 1951 (? VI)

R, L —*Liobole glabroides* R. & E. R. 1949 (III)

R, L —*Liobole glabra hiemalis* R. & E. R. 1949 (VI)

R, L —*Phillibole aprathensis aprathensis* R. & E. R. 1937 (III)

R, L —*Phillibole aprathensis moravica* Pribyl 1950 (III)

R, L —*Phillibole culmica* R. & E. R. 1937 (II)

? O —*Cystispina cystispina* R. & E. R. 1939 (VI)

? O —*Cystispina spatulata* (Woodward 1902) (VI)

R, F —*Typhloproetus schindewolfi* R. & E. R. 1919 (VI)

O　—*Typhloproetus microdiscus* R. R. 1913 (IV)

O　—*Typhloproetus subcarintiacus* R. R. 1913 (VI)

? O —*Typhloproetus dietzi* R. & E. R. 1951 (IV)

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[9] The writer found various free cheeks, one in place. They show no trace of facets.

O   —*Diacoryphe pfeifferi* R. & E. R. 1951 (IV)

O   —*Pteroparia columbella* R. R. 1913 (IV)

In modern arthropods there occur two tendencies of eye reduction (see G. de Lattin 1939). One is called centrifugal reduction, because the degeneration affects first the receptory parts of the visual organ (nerves) while the external parts (facets) still seem unaltered. The other one is the centripetal reduction. In this case the degeneration affects first the facets while the optical nerves remain unaltered. It is, of course, impossible to decide which of these tendencies is present in our proetids, or if possibly there occur both of them.

What we can observe is a general reduction in size of the visual area. The number of facets sometimes decreases. In other cases, the reduced visual area contains rather small facets. Together with the reduction of the visual area in size, a successive lowering takes place so that finally the facets are lying on the level of the surface of the free cheeks. In the late phases the number of facets becomes very small, and in the final phase does not remain any visible trace of facets (blindness).

Although this mode of reduction is recognizable in a general way, it does not seem that its different stages are specifically related to the stages of the reduction of suture and palpebral lobe. It seems rather that the rate of reduction of the palpebral lobe (expressed by the changes in the turning points γ, δ, and ϵ of the suture), and the rate of reduction of the visual area, are not specifically co-ordinated and that their relation differs in the various evolutionary branches of the Proetinae and Tropidocoryphinae.

The following list may show, however, in which way a general relation is statistically indicated between the reduction of the palpebral lobe (stages II-VI of the development of suture) and the obsolescence of the visual area. It is based on the above given list of 22 species with safely known middle and late stages of eye reduction and known visual area. It is to be expected that this general relation will become even more evident when our knowledge of the visual areas (separated free cheeks) of the species of the Proetidae will become more complete.

The list shows that, excepting two special cases (*Typhloproetus schindewolfi* R.

Reduction of palpebral lobe (stages of suture)	Reduction of visual area		Species with known visual area	
Stages	Facets	Relief	Number of species	Interpretation
VI	still facets	no relief	1	exceptional.
VI (with rudiment)	still facets	still low relief	1	exceptional.
VI	**without facets**	**no relief**	**7 (+2 ?)**	**"normal".**
V	without facets	still low relief	1	exceptional.
IV'	without facets	still low relief	1	exceptional.
IV	**without facets**	**already no relief**	**3 (+1 ?)**	**"normal".**
III	**still facets**	**already low relief**	**3**	**"normal".**
II	still facets	already no relief	1	exceptional.
II	relatively numerous facets	already low relief	1	?
II	**relatively numerous facets**	**high relief**	**numerous**	**"normal".**

& E. R. 1919 ; *Liobole hiemalis* R. & E. R. 1949), the final stage of the stretched suture (VI) is linked nearly always with complete loss of facets. These may disappear in earlier stages of the reduction of the palpebral lobe, but never before stage IV, whereas already in stage III the principal reduction of the palpebral lobe begins (obsolescence of ϵ). Furthermore, in stage II of some species, the visual area may remain large and rich in facets although the palpebral lobe is already remarkably reduced in size [p.e. : *Perliproetus marginatus* (v. Muenster 1842) ; *Carbonocoryphe bindemanni* R. & E. R. 1950, etc.]. Thus it seems that an intensification in reduction of the visual area is always preceded by intensified rudimentation of the palpebral lobe.

The reduction of the palpebral lobe starts in its posterior parts (step from stage I to stage II in both modes ; stretching of posterior branch in stage III of the *Piriproetus*-mode). This makes it probable that also the degeneration of the visual area may begin in the posterior part of the eye. On the other hand, E. Warburg pointed out that in trilobites "......it is (......possibly......) the posterior parts of the eyes which are earliest developed" (1925 : 47). Thus it appears that in general the posterior parts of the eyes have a special significance in the development.

The complete loss of facets has been called "blindness" (p. 83). It was presumed that in this phase the eye probably ceased to be functional in the sense that reception of images and measuring of distances became impossible (R. R. 1932 ; 845). It may be that a slight sensibility to light remained in some cases when the shell was thin and transparent (R. R. 1951 : 226), but in most cases the tuberculated sculpture of the shell suggests that even the transparency has decreased (R. R. 1951 : 226).

3. SIGNIFICANCE OF PROETID EYE REDUCTION

F. R. C. Reed (1898) pointed out that blinding of trilobites occurs in two different groups, one including primitive originally blind or small-eyed forms, while the other contains forms with an adaptive eye reduction. The "primordial original blindness" of trilobites has been refused by R. R.

(1939 : 1061/1062) because of the lack of evidence and because of the fact that in the Annelida the eyes can be highly developed or even subject to secondary reduction, although the Annelida are more primitive than the oldest trilobites. Thus there is little doubt that eye reduction in all cases of trilobites is secondary.

Theoretically, there are two ways to explain the origin of the eye reduction and blinding of the Proetidae. It could be supposed that it is an adaptation depending on environment and/or habit of life. The other possibility would be that eye reduction could be independent of environment, that it is caused by internal factors (mutative pre-adaptation). Morever, theoretically the entire phenomenon of blinding could be interpreted exclusively as a plain adaptation to a specific ecological niche or as a "phylogerontic" feature connected with the extinction of the Proetinae and Tropidocoryphinae.

It seems that neither of the explanations is satisfactory by itself, and that each represents an inadmissible oversimplification. A combination of both, however, appears to reach a higher degree of probability.

3a. EYE REDUCTION AND ENVIRONMENT

Many authors generally supposed that a relationship exists between the blinding in trilobites and conditions of environment.

One of J. Barrande's hypotheses (1852) suggested that eye reduction of trilobites is related to the occurrence in certain types of rocks and therefore to certain environments. This has been discussed by F. R. C. Reed (1898) and D. M. Delo (1937), both of them pointing out that blind trilobites occur in sediments of different type. Reed's opinion was that the trilobites with adaptive blindness "......are mostly local forms found only in a small and restricted area" and that the causes of their blinding may be represented by burrowing, by living in turbid water or in submarine cavities, while others may represent deep water forms. Delo understood the blinding of the Phacopidae as a "phylogerontic characteristic" which in its extreme was independent of environment. Recently, M. Schwarzbach (1950) interpreted the blindness of certain species of *Harpes* as being connected with life in deep water.

Text-Fig. 3—Supposed phylogeny of the branches of the younger Proetinae and Tropidocoryphinae that are subject to eye reduction. Based in part on R. & E. R. 1951.

[The detailed phylogeny of *Proetus* (*Proetus*) and *Proetus* (*Crassiproetus*) is not studied.]

Text-Fig. 3

15
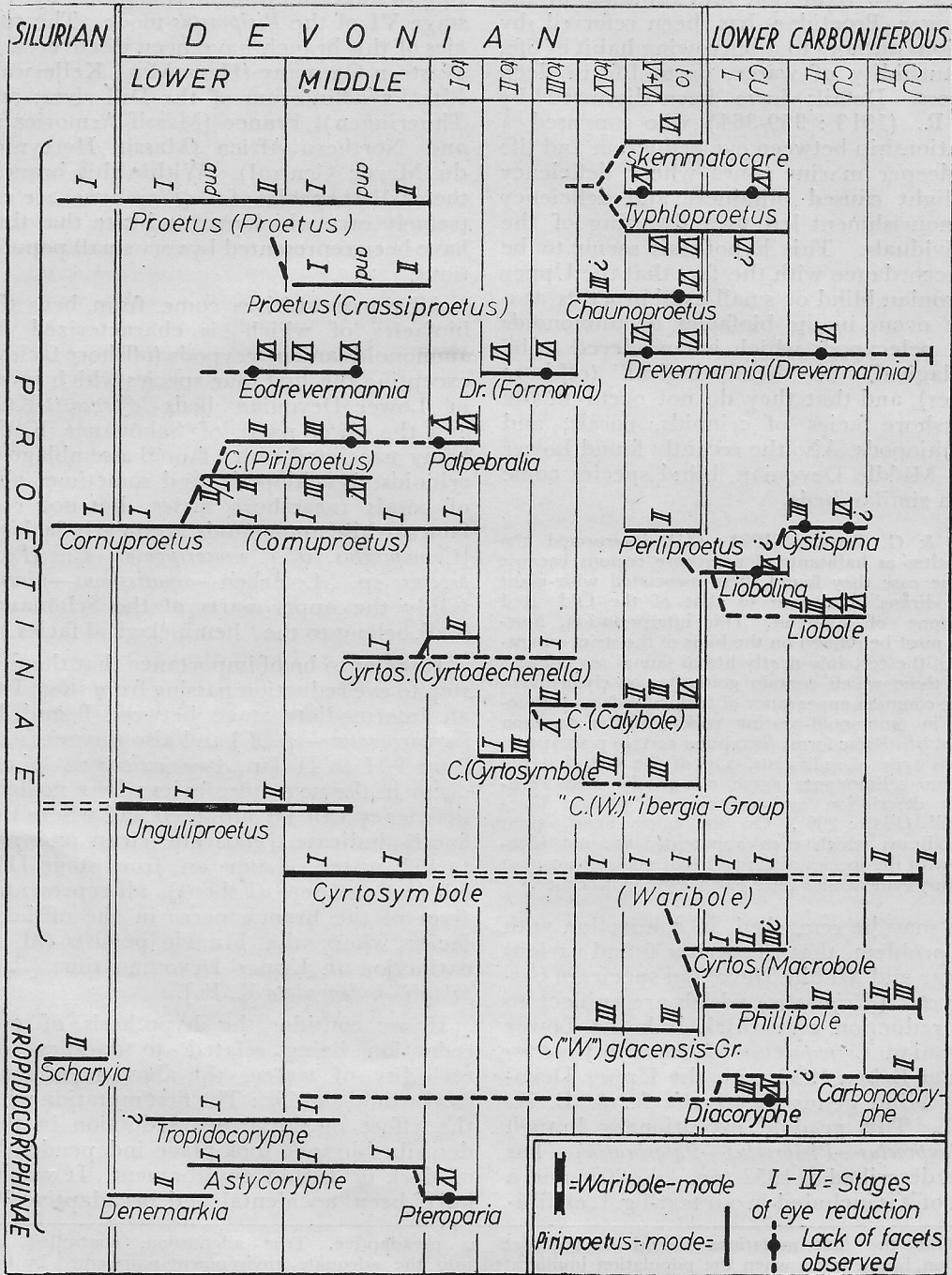
The eye reduction and blinding of the younger Proetidae has been referred by various authors to a burrowing habit of life, to turbidity of water, or to life in deep waters. Details have been discussed by R. R. (1913 : 359-364) who supposed a relationship between eye reduction and life in deeper marine zones where deficiency of light caused blindness, and deficiency of nourishment led to a dwarfing of the individuals. This hypothesis seems to be in accordance with the fact that the Upper Devonian blind or small-eyed proetids as a rule occur in the biofacies of ammonoids and pelecypods which is considered to be "pelagical" or "hemipelagical" (offshore facies), and that they do not occur in the nearshore facies of crinoids, corals, and brachiopods. Also the recently found Lower and Middle Devonian blind species come from similar beds.

H. & G. Termier (1952 : 421) interpreted the goniatites as habitants of nearshore regions because in one case they found them associated with giant arthrodirans analogous to that of the Old Red sandstone of England. This interpretation, however, must be refused on the basis of the strict separation of the certainly nearly litoral faunal assemblages from those which contain goniatites or clymeniids ; of the common appearance of tentaculitids and styliolinas in ammonoid-bearing rocks ; of the common lack of benthonic forms (excepting certain pelecypods) in this type of sediments, and of the fact that the concerned limestones agree completely with Pettijohn's description and criteria of "pelagic limestones" (1949 : 299). On the other hand, giant arthrodirans which even apparently are not identical with the species of the Old Red sandstone cannot give any evidence for their paleocologic significance.

It may be remarked, in connection with our problem, that the writer found various Lower and Middle Devonian species of *Cornuproetus (Piriproetus)* which are subject to eye reduction and which link the Lower Devonian *Cornuproetus (Cornuproetus) neocorrugatus* Erben 1952 with the Upper Devonian blind genus *Palpebralia* R. & E. R. 1927. This gradual evolutionary branch (*Cornuproetus—Piriproetus—Palpebralia*) has been described in 1952 (pp. 203-207) and a part of it is included in our text-fig. 1, exhibi-

ting all stages of eye reduction from stage I to stage VI of the *Piriproetus*-mode. The species of this branch have been discovered in Western Germany (Harz Mts., Kellerwald Mts., synclinorium of the Dill river, and Thueringen), France (Massif Armoricain) and Northern Africa (Massif Hercynien du Maroc Central). Within this branch, the earliest species of *C. (Piriproetus)* are extremely rare which may indicate that they have been represented by very small populations.

All representatives come from beds the biofacies of which is characterized by ammonoids and pelecypods (offshore facies), excepting the first four species which occur in Lower Devonian beds (*Zorgensis*-Kalk and the lower parts of Schönauer Kalk) being associated with a faunal assemblage of crinoids, brachiopods, and sometimes also of corals (nearshore facies, but not reef facies) while ammonoids are nearly lacking [*Cornuproetus (C.) neocorrugatus—C. (Piriproetus* sp. A. Erben—*ornatissimus—pirus*]. (Only the upper parts of the Schönauer Kalk belong to the "hemipelagical facies.)

It seems to be of importance that the first step to eye reduction passing from stage I to an intermediate stage between I and II [*neocorrugatus*—sp. A.] and also the next step from I/II to II [sp. *A—ornatissimus —pirus*] occur in the nearshore facies where no light deficiency can be supposed and where the corals indicate relatively clean and not turbid water. Later on, from stage III' [*C. (P.) amblyops* (Erben)], all representatives of the branch occur in the offshore facies where the branch persists till its extinction in Upper Devonian time [*Palpebralia nodannulata* R. R.].

If we consider the hypothesis of eye reduction being related to darkness or turbidity of water, the above-mentioned facts would signify : The first mutation with the effect of initial eye reduction in the described branch took place independently of dark or turbid environment. It would have been accidental and preadaptive [10].

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[10] Only the first mutations should be regarded as preadaptive. True adaptation, controlled by selection, began later, when the population immigrated into the adequate environment represented by the offshore facies. In a strict sense, every adaptation in its initial phases must be considered preadaptive. This is in accordance with the view of S. Wright (1949 : 365) who stated : "The available evidence indicates that these/.....mutations...../occur independently of physiological adaptations of the individuals. We are left with the hypothesis that phylogenetic adaptation is ultimately preadaptive". Ana-

While the initial evolutionary tendency continued, the later representatives of the branch immigrated into an environment of deficient light where selection would tolerate the previously initiated tendency to eye reduction.

Another hypothesis suggested a relationship between eye reduction and a burrowing habit of life. In many cases, burrowing arthropods in their morphology exhibit specific features which are adapted to this habit. In the above-mentioned branch, the following features could be interpreted as such adaptations : Reduction in size of the entire body, tendency to reduction of the sculpture ; tendency to transform the thickened anterior border of the cephalon into a flat ("shovel-like") rim ; and finally, eye reduction.

If we accept this second hypothesis, we obtain similar results : The first step to eye reduction precedes all the other tendencies. Also in this case the origin of eye reduction would be independent of the new mode of life (burrowing), which would have been chosen "to obtain the selection's tolerance" living in the darkness of the sediments.

Finally, the hypothesis of life in dark submarine cavities (p. 92) should be excluded in the present case. It could be taken into consideration : (a) if the populations have an extremely restricted geographical and geological range, (b) especially if they occur in a pure limestone reef facies which indicates an environment of abundant submarine cavities, (c) if the individuals are of small size and blind. In the *Piriproetus-Palpebralia* branch the criteria, (a) and (b) are by no means applicable and the characteristics of (c) may be interpreted in a different, above-described way.

[The trilobite family Isocolidae Whittington (1956 : 1193) shows all of these criteria and therefore the writer supposes that its representatives have been adapted to life in dark submarine cavities of certain reefs. Moreover, the writer wishes to call attention to the very remarkable fact that the blinding of this family is connected with the "*cryptophthalmus*-mode"

(see R. & E. R. 1926) which hitherto has been observed only in the phacopids].

For the above explained reasons the writer is inclined to believe that at least the eye reduction of the *Piriproetus-Palpebralia* branch occurred independently of environment or special habit of life, even if it appears adaptive by the fact that the populations later moved into the adequate environment or changed adequately their habit of life.

It might be that such independence in other cases is indicated by the fact that eye reduction (stage II) occurs also in *Proetus (Proetus)* although its species never leave the nearshore facies and do not exhibit features which could be interpreted as adaptations to burrowing. Also the eye reduction (stage II) of *Cyrotosymbole (Waribole)* seems to occur without related important changes in facies.

3b. EYE REDUCTION AND PHYLOGENY

Another possibility to obtain information about the significance of the proetid eye reduction is given by tracing the phylogeny of this group. This has been tried, in a general way, in text-fig. 4.

R. R. (1932 : 854) supposes that the Proetidae during future investigations will turn out to be a heterogenous collective group. The writer agrees as far as the Tropidocoryphinae and other subfamilies possibly may descend from other ancestors than the Proetinae, the family Proetidae (*sensu* Pribyl 1946) thus being possibly of polyphyletic origin. The relationship of these ancestors, however, must have been a very close one.

P. Hupé (1953) thinks that his Proetidae originated from the Asaphiscidae. E. Warburg (1925), based on Swinnerton, seems to believe in a phylogenetical connection of Proetidae and Olenidae. Henningsmoen (1951 : fig. 2) derives the Proetidae and Olenidae simultaneously from older Conocoryphacea. Recently, Whittington (1954 : fig. 1) derived the Proetidae from the Olenoidae or Solenopleurioidae. This view is shared by the writer who supposes that the ancestorship of the Olenidae is even more probable than that of the Solenopleurioidae. On this interpretation the text-fig. 4 is based (examples : *Triarthrus, Olenus, Liostracus*). The Olenidae are fairly

logous cases have been mentioned among blind cavernicoles (C. L. Hubbs 1938 ; Eigenmann 1909; and to a certain degree C. Kosswig 1936). For these cases, J. S. Huxley (1942 : 453-455) established the term "constitutional preadaptation" which seems of little help because it only avoids a decision and shifts it from the concerned descendants and direct ancestors to the not discussed ancestors of ancestors.
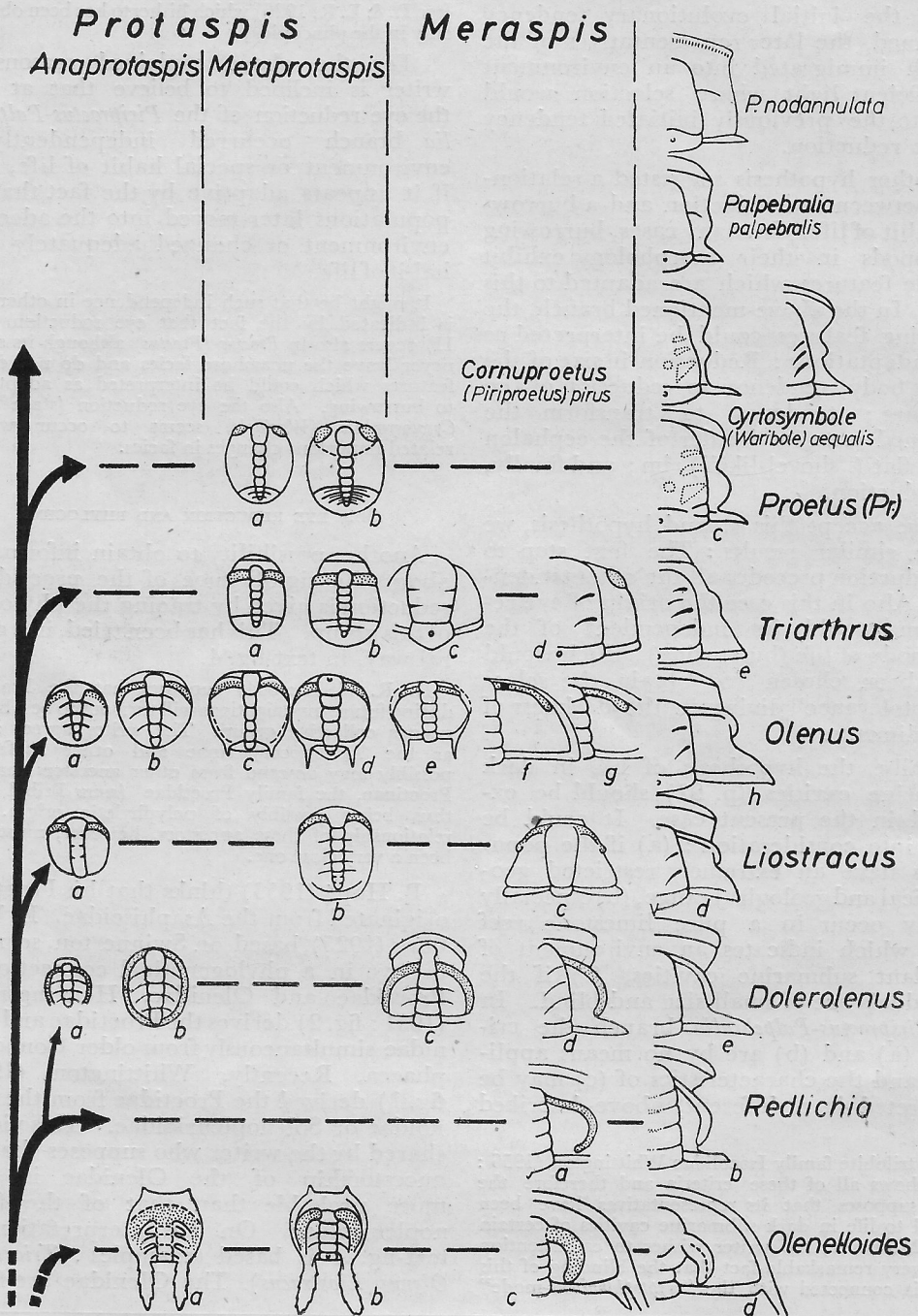
Text-Fig. 4

separated in Whittington's paper (1954 : fig. 1) from the Redlichioidae and the Olenelloidae, but we have to suppose that their ancestors probably resembled the latter to a considerable degree.

The text-fig. 4 tries to trace the behaviour of the eye of the proetids during its previous evolution, but, of course, it does not show the true phylogeny. It may give, however, a general idea about the approximative sequence of morphologic stages of eye development expressed by the sequence and ontogenies of a few representing genera of the ancestral groups (or groups which are close to the true ancestors).

This sequence shows the following evolutionary tendencies (see fig. 4) :

(*a*) Origin of a large palpebral ridge [p.e. : anaprotaspis ? of *Olenelloides*]

(*b*) Its separation from the protoglabella by furrows [p.e. : metaprotaspis ? of *Olenelloides*]

(*c*) Origin of palpebral lobe and visual area [11] [p.e. : late meraspids and holaspids of the Olenelloidae]

(*d*) Origin of a typical eye ridge [p.e. : meraspids and holaspids of the Redlichioidae]

(*e*) Eye still reaching posterior border furrow [p.e. : holaspids of Olenelloidae and primitive Redlichioidae]

(*f*) First reduction of eyes, beginning from the posterior parts [slightly indicated by some Redlichioidae. Beginning in late meraspids of the type of *Dolerolenus* and continuing during the ontogenies of Olenoidae of the types of *Liostracus* and *Olenus*]

(*f*1) The eye "migrates foreward" (shortening)

(*f*2) Posterior branch of suture remains without angle in ξ

Text-Fig. 4—Supposed general sequence of morphological stages which during phylogeny led to the Proetidae. Stages represented by genera with known or partially known ontogeny. Most drawings slightly simplified. In the meraspids and holaspids mostly only the cranidia or right sides of cranidia are reproduced. Palpebral ridges or eyes appear dotted, excepting in holaspids. Sizes generalized.

From lowermost row to upper rows :

a-d : Ontogeny of *Olenelloides gilberti* Meek (Olenelloidae—L. Cambrian).

a-b : Part of ontogeny of *Redlichia noetlingi* (Redlich) (Redlichioidae—L. Cambrian).

a-e : Part of ontogeny of *Dolerolenus* (Redlichioidae—L. Cambrian).

a-d : Part of ontogeny of *Liostracus* (Olenoidae —M. Cambrian).
    a-b : *L. ?* sp.   c-d : *L. linnarssoni* Broegger

a-h : Ontogeny of *Olenus* (Olenoidae—U. Cambrian).
    a-e : *O. gibbosus* (Wahl.)   f-g : *O. mundus* Lake

a-e : Part of ontogeny of *Triarthrus* (Olenoidae—Ordovician).
    a-b : *T.* sp.   c-e : *T. eatoni* (Hall) [=*becki* Green].

a-c : Part of ontogeny of *Proetus* (Proetidae—Ordovician to L. Carboniferous).
    a-b : *Proetus parviusculus* Hall

[*Olenelloides :* a-c after A. R. Palmer 1957 ; *Redlichia :* a-b after O. H. Schindewolf 1955 ; *Dolerolenus :* a-b from L. Stormer 1942 after Bornemann 1891, c-d from P. Hupe 1953 after Bornemann ; *Liostracus :* a-b after L. Stormer 1942, c-d after E. Warburg 1925 ; *Olenus :* a-e after L. Stormer 1942, f-g from E. Warburg 1925 after Lake 1907 ; *Triarthrus :* a-b from L. Stormer 1942 after Beecher 1895, c-d after Walcott 1918 ; *Proetus :* after Beecher 1895.]

[In "a" of the *Dolerolenus* row, the posterior border has not been included in the drawing because the interpretation which is given for this part by the original figure, appears improbable. Eyes have not been reproduced in "c" of the *Triarthrus* row because the corresponding region in Walcotts original figure is not sufficiently clear.]

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[11] In the late meraspis of *Olenellus*, Palmer (1957) observed a subdivision of the palpebral ridge. Facets on the visual area of the Olenelloidae have been observed by F. Raw (1957 : 152/153) and others.

(g) Reduction of eye ridge [p.e. : early meraspids of *Triarthrus*-type Olenoidae and all following forms]

(h) True migration of eyes toward anterior border of cephalon [occurred between the holaspids of Olenoidae without eye ridge, and early metaprotaspis of *Proetus*]

(i) Migration of eyes backwards [late metaprotaspis of *Proetus* to holaspis of this genus]

(j) Second reduction of eyes beginning from the posterior parts [numerous branches of younger proetids]

    (j 1) The eye secondarily "migrates foreward" (shortening)

    (j 2) Posterior branch of suture secondarily without angle in ξ [stage II of *Waribole*-mode ; stages V-VI of *Piriproetus*-mode]

    (j 3) Reduced eye can undertake a true migration towards anterior border of cephalon [*Liobole*]

    (j 4) Eye ridge can secondarily reappear [some *Palpebralia*, a.o.].

From this general sequence of morphological stages which during the phylogeny led to the Proetidae, it becomes evident that the rather large and posteriorly situated "normal" eye of the Proetidae is a secondary feature, and that the eye reduction of the Proetidae is the second eye reduction during the evolution of the genealogic tree in question. Moreover, it seems that eye reduction is a common evolutionary tendency of the entire tree, in which it occurs as an incomplete reduction already from Lower Cambrian to Ordovician time and as incomplete and complete reduction during Devonian and Lower Carboniferous. It appears difficult to explain the origin of such tendency exclusively by dependence on a certain type of environment because it does not seem probable that such conditions persisted during nearly the whole of Lower Paleozoic.

3C. EYE REDUCTION AND EXTINCTION

The tendency to eye reduction already had existed within the proetids of Ordovician times (p.88), but no case of blindness is known. Stages passing beyond stage II of reduction apparently appeared first in the late Lower Devonian, as text-fig. 5 shows. From this figure it becomes evident that from Lower Devonian to early Lower Carboniferous, within the younger Proetinae [12] the predominance of "normally"-eyed species was replaced by a predominace of forms showing reduced eyes or blindness. Since the sediments of the offshore facies (facies of ammonoids) become very common in the Upper Devonian, the change in the predominance could be explained by the continuous expansion of this facies which offered a tolerant or even favourable environment to the species with rudimentary eyes.

The writer supposes that the expansion of the offshore facies was caused by general bathymetric changes which in parts of Europe may have been connected with the continuous deepening of the Hercynian (Variscean) geosyncline. Furthermore, it should be mentioned that the Proetinae with reduced eyes apparently occur mostly (but not exclusively) in Europe.

Text-Fig. 5—Distribution of species and subspecies of the younger Proetinae which are subject to eye reduction.

(Includes only species, subspecies and "aff.-forms" with known palpebral region. The data for Lower and Middle Devonian may be incomplete, but only to a tolerable degree).

Directions for use :

Within each time unit, the whole of the covered horizontal distance gives the total number of present species, etc. Within this, the sum of distances covered by a specific hatching shows the number of species, etc., which correspond to that stage of eye reduction which is expressed by the corresponding pattern of hatching. For determination of numbers and stages, use the scale and the explanation present in the figure.

To give an example : Distance between a-b (Upper Devonian) = Total number : 54 ; forms in stage I ("normally"-eyed) : 12 ; forms in stage II : 9 ; forms in stages III—IV : 33.

(Graphical method after A. H. Mueller 1955.)

[12]The Tropidocoryphinae have been excluded from fig. 5 because of the still incomplete knowledge of this subfamily.
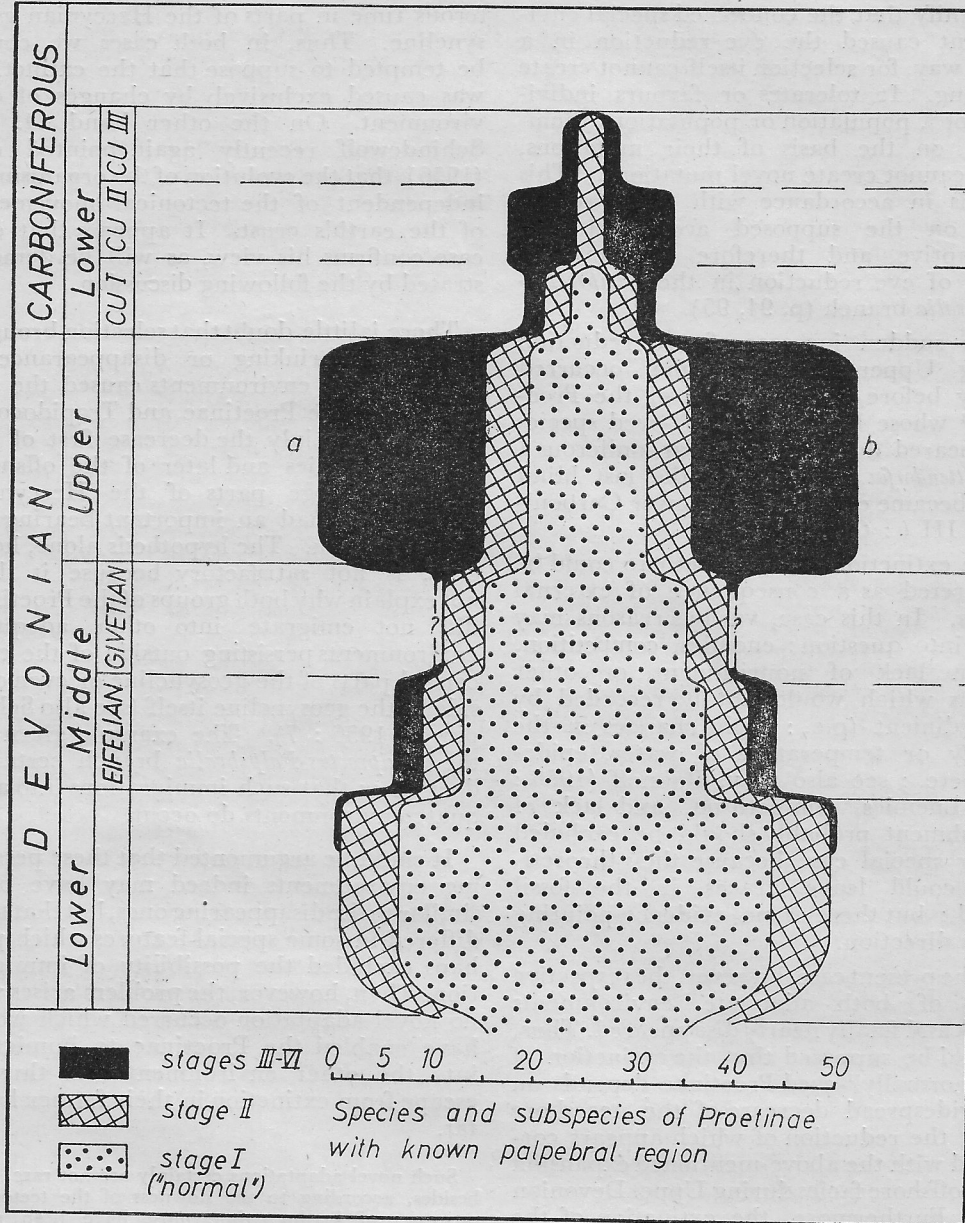
Text-Fig. 5

The above-given explanation of the increase of eye reduction, however, does not signify that the concerned special environment caused the eye reduction in a direct way, for selection itself cannot create anything. It tolerates or favours individuals of a population or populations themselves, on the basis of their mutations, but it cannot create novel mutations. This view is in accordance with our observations on the supposed accidental and preadaptive, and therefore independent, origin of eye reduction in the *Piriproetus-Palpebralia* branch (p. 94, 95).

The sudden increase of eye reduction during Upper Devonian time, occurred shortly before the extinction of the Proetinae[13] whose last "normally"-eyed species disappeared during Lower Carboniferous I (: *Gattendorfia* stage) while the last blind forms became extinct in the Lower Carboniferous III (: *Goniatites* stage).

The extinction of the Proetinae could be interpreted as a consequence of external factors. In this case, various reasons may come into question : enemies, competition, sudden lack of nourishment, or other reasons which would not be recorded by the sediment (p.e. : slight changes in the salinity or temperature of water, epidemics, etc. ; see also S. v. Bubnoff (1956 : 24). Enemies, competition, and lack of nourishment probably should be excluded in our special case because they theoretically could leave traces in the fossil record ; but there is no evidence pointing in this direction.

In the present case, however, the respective areas of both adequate environments shrank and finally nearly disappeared. Thus, it could be supposed that the extinction of the "normally"-eyed Proetinae depends on the widespread decrease of the nearshore facies, the reduction of which appears correlated with the above-mentioned expansion of the offshore facies during Upper Devonian time. Furthermore, the extinction of the group which was blind or had rudimentary eyes and which represents the last Proetinae, may be connected with the final reduction of the offshore facies which was caused by the orogenetic events taking place during late Lower and Upper Carboniferous time in parts of the Hercynian geosyncline. Thus, in both cases we could be tempted to suppose that the extinction was caused exclusively by changes of environment. On the other hand, O. H. Schindewolf recently again pointed out (1956), that the evolution of the organisms is independent of the tectonical movements of the earth's crust. It appears that our case confirms his view, as will be demonstrated by the following discussion.

There is little doubt that selection brought about by shrinking or disappearance of the adequate environments caused the extinction of the Proetinae and Tropidocoryphinae. Certainly the decrease first of the nearshore facies and later of the offshore facies in large parts of the Hercynian geosyncline, had an important bearing on this extinction. The hypothesis alone, however, is not satisfactory because it does not explain why both groups of the Proetinae did not emigrate into other adequate environments persisting outside of the concerned parts of the geosyncline or even outside of the geosyncline itself (see also Schindewolf 1956 : 7). The example given by the *Piriproetus-Palpebralia* branch certainly does show that such immigrations into adequate environments do occur.

It could be argumented that these persisting environments indeed may have been similar to the disappearing ones, but that they differed in some special features which perhaps excluded the possibility of immigration. Then, however, the problem arises why no novel adaptation occurred which would have enabled the Proetinae to immigrate into the other environment and thus to escape from extinction in their former habitat.

Such novel adaptations certainly are not rare, and, besides, according to the slowness of the tectonical processes of folding, time must have been more than sufficient to produce a novel mutation adaptable to the other environmental conditions. Moreover, S. Wright (1949 : 380) explained, how in analogous cases a change of environment can be carried out within relatively short times.

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[13] *Permoproetus* Toumansky probably is homoemor- phous, and seems not to belong to the subfamily **Proe**tinae.

The same problem remains if we disregard the reduction of adequate facies, and instead accept the other conditions which above have been mentioned as possible factors of selection.

The question asked above could be formulated even in an absolutely general manner, namely, in the case of every extinction, and the only logically sound answer would be that novel adaptations apparently were impossible in the concerned phase of phylogeny.

Thus it becomes evident that a satisfactory explanation of the extinction cannot be given by external factors only. If we avoid the exaggerated eagerness of some authors of explaining every time almost everything nearly exclusively by selection, we have to admit that selection and changes of environment may be the last effecting causes for extinction, but not the original ones. These are represented by the failure to produce novel adaptive tendencies in late phylogenetic phases. Till now, the exact mechanisms are not known which led to this failure[14], and so the corresponding term "typolysis" (Schindewolf, see 1950) is rather a descriptive one, but it is based on experience obtained by observation of the concerned phenomenon in different groups of animals.

It has been mentioned (p. 100) that blinding increased shortly before the extinction of the Proetinae, and it seems that both are related. It may be that blinding was an additional factor of extinction in branches which terminate with stage VI of blinding (see text-fig. 3). On the other hand, in branches which in spite of complete blindness (stage VI) persist through relatively long times [p.e. *Drevermannia* (*Drevermannia*), *Eodrevermannia*, *Typhloproetus*] and also in the "normally-eyed" branches and branches with incomplete eye reduction, this explanation seems less probable. In these instances, the above-mentioned disappearing of adequate environments in combination with inability to change the adaptive tendency, may give a better explanation. Thus, blinding cannot be interpreted, in a strict sense, as the exclusive internal cause for extinction. On the other hand, text-fig. 5 indicates clearly a relationship between both.

The writer believes that the increase of blinding probably should be conceived as a symptom of the typolytic phase [15] of the late Proetinae (and Tropidocoryphinae) during Upper Devonian and Lower Carboniferous :

The incipient eye reduction of the Proetinae most probably was accidental and preadaptive (p. 94), and therefore independent of environment. In the original environment of nearshore facies it must have been of negative selective value.

When the populations immigrated into the adequate environment represented by the offshore facies, a certain harmony between evolutionary tendency and environment was established, based on the tolerance granted by the environment, and eye reduction may have become an indifferent or possibly advantageous feature with regard to selection. Later, when during Upper Devonian times the nearshore facies shrank, the novel acquired characteristic of eye reduction even happened to become an adaptive characteristic of positive selective value, whereas the "normally"-eyed species became extinct. In this stage, eye reduction should be regarded as an adaptive specialisation to a specific ecological niche. During this and the preceding phase it advanced orthogenetically. [16]

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[14] These mechanisms certainly will have nothing to do with mysterious forces of vitalistic kind. To use descriptive terms, the mentioned failure appears as a result of orthogenetical (see footnote 16) adaptation which leads to overspecialisation (Schindewolf, see 1950). These phenomena have not been observed by geneticists probably because they examine only the diminutive present sector of an extremely long ranged phylogeny.

[15] The term "phylogerontic" (among others : Delo 1937 ; R. & E. R. 1951, etc.), should be strictly avoided because it could be interpreted as implying a vitalistic element ("-gerontic").

[16] Orthogenesis has been denied by several geneticists. If we use this term in a descriptive sense (not as an intended explanation), orthogenesis is, however, an observed phenomenon which is very common in the fossil record. This phenomenon may be a result from previous preadaptive tendency, orthoselection, and "irreversibility" of evolution. C. Kosswig has explained (1945 : 142 ; 1947 : 42/43) why orthogenesis is not in contradiction to the principles of genetics. [The doctrine of irreversibility has been refused many times. In fact, incomplete reversions (concerning one or a few characteristics) are not rare. On the other hand, complete reversions theoretically could occur, but practically they do not or nearly never. Thus, "irreversibility" is not a law, but a statistically conditioned fact with almost no exception, based on the relative scarcity of reversive mutations of a single gene in comparison with the mutation rate of all other genes. A genetically based explanation results from some of C. Kosswig's statements (1945 : 142/143 ; 1947 : 41.)]

16

By the approach of farther reaching orogenies of the Variscean era, the adequate environments tended to disappear, and the populations of Proetinae with rudimentary eyes and of blind forms proved not to be able to produce novel mutations for adaptive tendencies which would have enabled them to move into still persisting other environments similar to the original ones. Thus the specialisation, once having passed a certain treshold, turns out to have become an overspecialisation which enabled the selection to execute the definitive extinction.

The described features of eye reduction of the Proetinae coincide completely with the criteria which O. H. Schindewolf recognized and described (1950, etc.), as characteristic of typolysis.

The typolysis of the Proetinae (and to a less degree, also of the Tropidocoryphinae) is connected with the interesting phenomenon of common appearance of "atavistic" and aberrant features :

(1) In *Skemmatocare* (Text-fig. 2d) and *Pteroparia* (Text-fig. 2e) the anteri or branch of the facial suture is bent laterally outward, respectively backward, in an extreme manner which is highly aberrant. In *Pteroparia* this may be an exaggeration of a common phyletic tendency of the Tropidocoryphinae, but in *Skemmatocare* it appears extremely unusual among the Proetinae. This feature remembers an evolutionary tendency of the Ordovician Amechilidae (Text-fig. 2a, b) and of the Cambrian *Entomaspis* (Text-fig. 2c), but as both are not related to the Proetidae, *Skemmatocare* and *Pteroparia* only offer cases of aberrant homoeomorphy.

(2) In *Scharyia micropyga* (Text-fig. 2f)—which probably represents a short trend of the Tropidocoryphinae, w is shifted laterally far outward. This clearly is an "atavistic" reminiscence of the olenoid ancestors (Text-fig. 2k), for this feature has been abandoned previously by the typical Proetidae (including Tropidocoryphinae). The aberrant transverse course of the posterior branch of the suture may be called homoeomorphous with regard to the Cambrian *Cedaria* (Text-fig. 2g). It simulates the "type pseudoproparial ou cedariforme" of suture, mentioned by P. Hupe (1953 : 54).

(3) The *Waribole*-mode of eye reduction (Text-fig. 2h ; fig. 1-II) is a clearly "atavistic" feature, in which the lack of the turning point ξ of the suture reappears, which is typical of the olenoid ancestors (Text-fig. 2k).

(4) The late stages (V-VI) of the *Piriproetus*-mode of eye reduction (Text-fig. 1 V-VI) are highly "atavistic" in the same sense (cf. fig. 2k).

(5) The reappearance of an indicated eye ridge in some *Cornuproetus* (*Piriproetus*), *Palpebralia*, etc. (Text-fig. 1— III, IV', V, VIb), is conspicuously "atavistic" with regard to all proetid ancestors [cf. (g) and (j4) on p. 98].

(6) The true migration of the eyes to the anterior border of the cephalon which is slightly indicated in *Liobole,* is the renewal of an ancient tendency which appears as a phylogenetical step from the holaspids of advanced Olenoidae (of *Triarthrus*-type) to the early metaprotaspis of *Proetus* [cf. (h) and (j3) on p. 97, 98].

(7) The shortening of the proetid eye, beginning from its posterior parts ("migration foreward") is "atavistic" because it repeats a process already having taken place in the ancient ancestors or groups which are closely related to these [cf. (f) and (j1) on p. 97, 98].

(8) Even the eye reduction itself, in proetids is "atavistic" in the same sense [cf. (f) and (j) on p. 97, 98].

(If we are consequent, we would have to call "atavistic" even the "normal" proetid eye ; it nearly reaches the posterior border furrow of the cephalon, in the same manner as in the ancient Olenelloidae and some Redlichioidae to which the unknown oldest ancestors of the proetids must be related, representing analogous morphologic stages.)

The common occurrence of "atavistic" features during the typolysis of the Proetinae finds its equivalent in the typolytic phases of the Ammonoidea. During the typolysis of the Ceratitacea, a reduction and secondary simplification causes an "atavistic" suture (*Rhabdoceras*, *Cochloceras*) which simulates the sutural type of the goniatitic ancestors. In the late Ammonitacea, the same process takes place, for in the "atavistic" suture of the Cretaceous pseudoceratites (*Engonoceras*, *Tissotia*, etc.), the principal features of the ceratitic ancestors reappear. Finally, the tendency of some typolytic Ceratitacea and Ammonitacea to become evolute, in all concerned morphological stages (secondarily crioceracone, cyrtoceracone, and orthoceracone), is clearly "atavistic" if we consider the way of evolution from the nautiloids to the goniatites. It may be that such "atavisms" are caused by growth restrictions possibly due to some specific behaviour of the rate genes as was pointed out by J. S. Huxley (1942 : 527/528) in the case of the suture of the ammonoids. Unfortunately, it is unknown which relationship exists between the latter and late stages of phylogeny.

In the present case, there is no secondary inadaptive spinosity or any other feature which could be interpreted as typolytic, excepting the eye reduction. Moreover, there is no phyletic increase of size, our case representing, thus, an exception and even the contrary of the phenomenon which is known as "the rule of Cope". On the other hand, all the above-described "atavistic" and/or aberrant features are related

to the eye and to the suture which depends on the eye. Thus, typolysis in the Proetinae and Tropidocoryphinae becomes evident with regard to only one organ, which is the eye. Therefore, it should not be astonishing if in other eventual cases of extinction, typolysis would not become recognizable at all, because it concerns exclusively one or a few organs or features which accidentally may not remain preserved in fossils, or because it happens to concern customs and habits of life which do not leave traces in the fossil record.

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