

SYSTEMATICS AND EVOLUTION OF
PHACOPS RANA (GREEN, 1832) AND
PHACOPS IOWENSIS DELO, 1935
(TRILOBITA) FROM THE MIDDLE
DEVONIAN OF NORTH AMERICA

NILES ELDREDGE

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ABSTRACT

TWO TRILOBITE SPECIES, *Phacops rana* (Green, 1832) and *Phacops iowensis* Delo, 1935, from the Middle Devonian of North America, are analyzed in detail from the point of view of geographic and stratigraphic variation. A purely morphological, as opposed to biostratigraphic, approach is used in analyzing relationships among subtaxa of the two species. Subsequent comparison of the relative sequence of inferred evolutionary events with documented biostratigraphic distributions allows an analysis of trends (biostratigraphic character gradients), character displacement between the two species, and mode of origin of the subtaxa.

The schizochroal eye of these species is the most important anatomical complex in terms of both intrapopulational and interpopulational variation and species discrimination. Lens number per eye may be broken down into number of dorsoventral files (vertical columns of lenses) and number of lenses per dorsoventral file. The adult population number of dorsoventral files per eye in *Phacops* is reached early in ontogeny and is stabilized; the number of dorsoventral files is the most consistently reliable criterion for discrimination of the two species.

Throughout its history, *P. iowensis* had 13 dorsoventral files in normal adults. This species belongs to a native North American phacopid lineage that can be traced back at least as far as the Gedinnian ("*Phacops*" *logani* Hall).

Phacops rana, morphologically closest to *P. schloth-eimi* (Bronn) from Europe and elsewhere, has from 15 to 18 dorsoventral files. Most of the history of species involved the reduction from 18 to 15 files;

the reduction is an allopatric phenomenon, involving transitional populations acquiring a reduced number of dorsoventral files on the eastern margin of the craton (exogeosyncline), which subsequently invade the cratonal interior. Other evolutionary changes in the *P. rana* lineage appear to be phyletic trends.

The two species are nearly mutually exclusive, though coeval and their geographic ranges overlap considerably. Although *P. iowensis* occurs from Iowa to New York, it was confined to the Michigan Basin for the larger part of its history. *Phacops rana* is found from New York south to Virginia and west as far as Iowa. *Phacops iowensis* was by far the more stable through time; it is invariably rare, and generally confined to purer limestones. The one case of sympatry between *rana* and *iowensis* occurs in the Hungry Hollow Formation of Ontario, resulting in morphological changes in the two species which are best explained as character displacement. The *P. rana* lineage as a whole converged on *iowensis* in number of dorsoventral files and in many ornamental features; the convergence was closest in the Taghanic.

The distributions of, and interactions between, *Phacops rana* and *Phacops iowensis* are best explained if the two taxa are considered true "bio-species." Although the little change that occurred within the *iowensis* lineage seems to have been phyletic in nature, the allopatric model is necessary to account for the more important evolutionary changes in *P. rana*.

Five subspecies of *Phacops rana*, including *P. rana paucituberculata*, new subspecies, and three subspecies of *P. iowensis*, are recognized.

INTRODUCTION

INVESTIGATIONS of evolutionary phenomena on the species level are again coming into vogue in paleontology. This renewed interest stems predominantly from the emphasis on populations in the "New Systematics," the realization that large samples of fossils, particularly of marine invertebrates, spanning broad geographic areas and thick stratigraphic sequences are available, and the relatively recent appearance of sophisticated multivariate statistical routines performed on computers. The present study gives the results of a detailed consideration of the variation and evolution within two coeval species of trilobites whose geographic ranges overlap. Taken together with other similar studies that have appeared recently, it is hoped that the feasibility of studying micro-evolutionary phenomena in the fossil record may be demonstrated.

Quantitative techniques, especially various forms of factor analysis, are used extensively in parts of the present report. By now these techniques are conventional and need no further discussion, although the basic elements of the multivariate models actually used are explained in the text. The study does stray a bit from convention in that a biostratigraphic approach for phylogenetic reconstruction is abandoned in favor of an analysis of relationships based strictly on morphological features determined to be "primitive" or "advanced." A purely "cladistic" approach to the systematics of fossil taxa need not debar application of evolutionary models to the explanation of phylogenetic patterns in the fossil record. This point of view is elaborated on in the text. A detailed application of the allopatric model to certain elements of the data presented here is contained in Eldredge (1971).

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I am deeply indebted to Dr. H. B. Rollins of the University of Pittsburgh who originally introduced me to the Hamilton fauna of central New York. Our discussions on *Phacops* and other faunal elements, as well as the physical stratigraphy of the Middle Devonian of New York, were of great help throughout the course of this study. Dr. R. L. Batten of the American

Museum of Natural History and Columbia University devoted many hours to discussing various evolutionary implications, as did Dr. N. D. Newell of the same institutions. I am also grateful for conversations with Mr. J. C. Boylan, of Columbia, Dr. L. Marcus of Queens College, Dr. R. M. Finks of Queens College, and Dr. G. J. Nelson of the American Museum of Natural History.

To Dr. D. V. Manson of the American Museum I owe a special debt of gratitude. Dr. Manson wrote the factor analysis program MUST used extensively herein, and arranged for the analysis of the data. He also reinitiated me into the intricacies of factor analysis, thereby greatly increasing my knowledge of this multivariate procedure.

Dr. E. N. K. Clarkson of the University of Edinburgh has given me instructive advice on the nature of phacopid eyes and has also critically reviewed portions of an earlier version of the manuscript.

I wish to thank the following people for arranging loans of specimens from their respective institutions: Dr. S. J. Gould, Museum of Comparative Zoology, Harvard University; Mr. C. Kilfoyle, New York State Museum; Dr. Steven W. Mitchell, Wayne State University; Dr. E. C. Stumm, University of Michigan Museum of Paleontology; Mr. F. J. Collier, United States National Museum, Smithsonian Institution; Dr. R. Linsley, Colgate University; and Mr. H. Strimple, State University of Iowa. Mr. Strimple also helped to clarify the stratigraphic positions of many of the specimens in the Iowa collections.

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Mr. David R. Eldredge gave very helpful advice and assistance in computation. Mr. Richard C. Eldredge served as field assistant for portions of the summers of 1966 and 1967; his enthusiasm, diligence, and sharp eyes provided

many of the better specimens of *Phacops* used in this study.

Finally, my wife, Michelle, who has been forced to live in a world colored by *Phacops* for several years, deserves much of the credit for the final appearance of this study. As field assistant her eyes were unerring and her spirit unflagging. Her encouragement throughout the subsequent months of analysis and final preparation of the present report made the way far easier for me. This study is largely attributable to her patience and is dedicated to her.

The contents of the present paper are drawn largely from my Ph.D. dissertation at Columbia University completed in 1969. Research was

supported by a National Science Foundation Graduate Fellowship and funds for field work granted by the Department of Geology, Columbia University.

ABBREVIATIONS

AMNH, the American Museum of Natural History,
Department of Invertebrate Paleontology
MCZ, Museum of Comparative Zoology, Harvard
University
NYSM, New York State Museum, Albany
SUI, State University of Iowa
UMMP, University of Michigan Museum of Paleon-
tology
USNM, National Museum of Natural History,
Smithsonian Institution

MIDDLE DEVONIAN STRATIGRAPHY

THE MIDDLE DEVONIAN of eastern and central North America provides an excellent source of material for studies of geographic variation and evolution. The rocks are well known and correlations are reasonably secure. There is a wide range in types of sediments deposited synchronously in different regions, and a great deal of time (some eight to 10 million years) was available for evolutionary change. An added advantage to the present study is that *Phacops* has rarely been utilized for biostratigraphic purposes, removing any possible circularity from the framework of relative time.

Both the time-stratigraphic classification of Middle Devonian rocks of the United States and correlation with European series have undergone revision in recent years and are not entirely stabilized. The "Hamilton" (comprising the Marcellus, Skaneateles, Ludlowville, and Moscow formations as revised by Cooper, 1930) and the overlying Tully and "Chemung" formations and their lateral equivalents, are the *Phacops rana* and *P. iowensis*-bearing rocks. Cooper et al. (1942) classified these rocks as the Erian series, subdivided into the Cazenovia, Tioughnioga, and Taghanic stages (see fig. 1). The lower portion of the Cazenovian, corresponding to the Marcellus and its equivalents, was considered Eifelian, and the rest of the Erian was allocated to the Givetian.

A slightly rearranged classification is given by Rickard (1964) and adopted here (fig. 1).

The main change is the downward extension of the Givetian to include the entire Cazenovian and the reallocation of the Taghanic to the younger Frasnian series. Thus under currently accepted terminology, there is no convenient term to embrace Cazenovia, Tioughnioga, and Taghanic. The Taghanic is Frasnian on the basis of European ammonoid zones, and although containing new, European-derived faunal elements (e.g., *Scutellum*), clearly is faunistically closer to the underlying Hamilton rocks than to the rocks subsequently deposited. On this basis, the classification of Cooper et al. (1942) is perhaps the more convenient as it provides a term ("Erian") which exactly corresponds to the *Phacops*-bearing rocks herein discussed. However, accurate correlation with European rocks is clearly desirable to facilitate close comparisons of related taxa, and as conodonts and ammonoids indicate a correlation more along the lines propounded by Rickard (1964) than by Cooper et al. (1942), Rickard's classification is accepted here. For convenience, the term "Middle Devonian" as used throughout this study stands for Cazenovia, Tioughnioga, and Taghanic stages.

Although a study of geographic and temporal variation must necessarily have an independently established time framework on a regional basis, the Middle Devonian of the eastern and central United States is far from totally understood.

Disagreements on the correct correlation of

COOPER, et al., 1942			N.Y.S. SECTION	RICKARD, 1964		
GIVETIAN	ERIAN	TAGHANIC	TULLY	TAGHANIC	SENECAN	FRASNIAN
		TIOUGHNIOGA	MOSCOW	TIOUGHNIOGA	ERIAN	GIVETIAN
			LUDLOWVILLE			
		CAZENOVIA	SKANEATELES	CAZENOVIA		
EIFELIAN	MARCELLUS					

Fig. 1. Comparison of the time-stratigraphic classifications of Middle Devonian rocks by Cooper et al. (1942) and Rickard (1964).

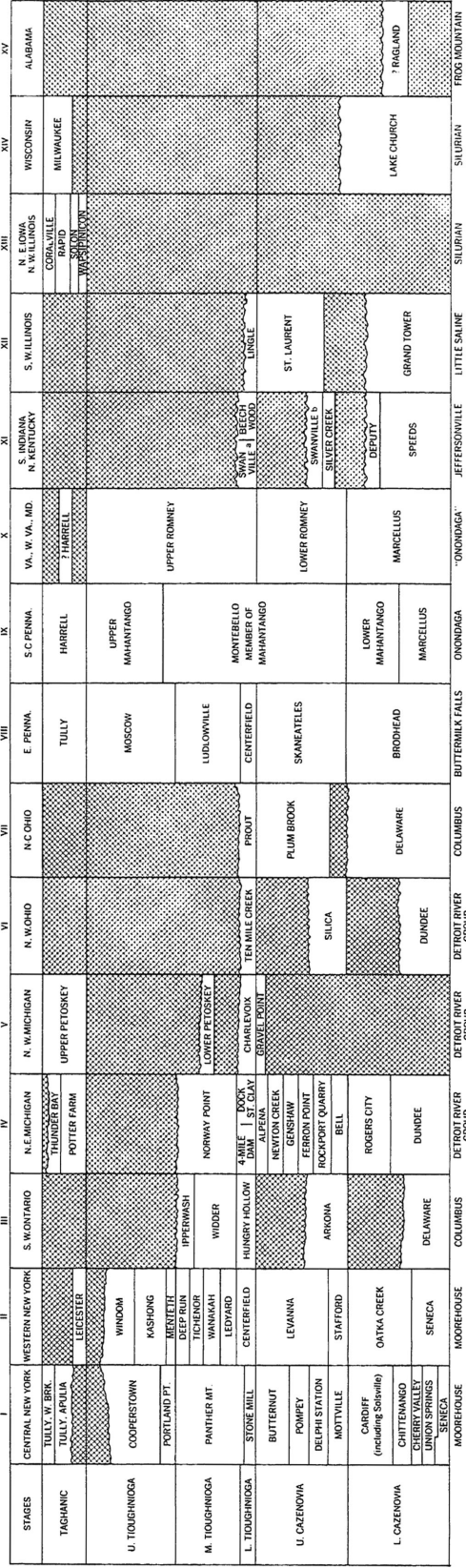


FIG. 2. Correlation of selected Middle Devonian sections in North America

I, II—after Rickard, 1964. Mottville and Stafford are considered as the lowest members of the Skaneateles Formation, not as highest members of the Marcellus Formation as in Cooper et al. 1942. III—after Anon., 1956, and Ehlers et al. 1952. IV—after Ehlers et al. 1952. V—after Cooper et al. 1942. VI—after Ehlers et al. 1952. VII—after Cooper et al. 1942. VIII—after Cooper et al. 1942. IX—after Ellison, 1965. X—after Cooper et al. 1942. XI—after Cooper et al. 1942; Campbell, 1942; Stumm, 1964a. Stumm considered the Swanville^a a facies of the Beechwood Formation. Cooper et al. and Campbell consider the Swanville^b to be older than the Beechwood, and thus Cazenovian. XII—modified after Cooper et al. 1942. XIII—modified after Cooper et al. 1942. XIV—after Cooper et al. 1942. XV—after Cooper et al. 1942. Omit Beauvais sandstone and Misenheimer shale. XIII—after Cooper et al. 1942. XIV—after Cooper et al. 1942. XV—after Cooper et al. 1942.

A “?” denotes that the time-stratigraphic position of a unit is in doubt.

Cross-hatching denotes absence of rock units.

rocks of certain areas with the standard of the Chenango Valley in New York are common, and a certain amount of choice exists between two or more slightly variant correlations proposed by different workers. The works of G. A. Cooper over the past 40 years serve as the starting point for all discussions of Middle Devonian strata of the eastern and central states and southwestern Ontario. Figure 2 shows the major stratigraphic sections investigated in the present study. Although Cooper et al. (1942) is the main source, the most recent work in each area has been incorporated into the chart.

A noticeable feature of the Middle Devonian of eastern and central North America is the virtual absence of Tioughnioga sediments west of the Buffalo arch. The only exceptions are the widespread basal Tioughnioga "Centerfield" faunas and the Widder, Norway Point, and Lower Petoskey formations of southwestern Ontario and eastern and western Michigan. No proved Moscow equivalent exists west of Buffalo, New York where the Windom member thins to 12 feet on the eastern shore of Lake Erie.

The stratigraphic section, then, is far more complete in the exogeosyncline on the eastern margin of the continent than it is on the cratonal

interior to the west. The rock sequences in the east are also much thicker and evidently represent a more complete record of time.

The well-known clastic wedge of the eastern exogeosyncline of the Middle Devonian thins and pinches out to the west, with sandstones and siltstones giving way to calcareous shales and purer limestones. Occasional limestones do occur in the east and form the basis of most of the understanding of the physical stratigraphy of the Hamilton Group, particularly in New York. But in general, within any one recognizable biostratigraphic unit of short duration, there is a great range of sedimentary environments preserved. The direction of greatest sediment variation is along a line normal to the roughly north-south strike of the ancient shoreline in the east running west to Michigan. It is along this axis that the greatest amount of variation within both species and subspecies of *Phacops* is evident. There is much less sediment and biologic variation parallel to the shoreline within the Appalachian system and within other local tectonic areas such as the Michigan Basin.

A complete locality list for specimens used is given in Appendix 2.

MORPHOLOGY AND RELATIONSHIPS OF THE BIOSPECIES *PHACOPS RANA* (GREEN, 1832) AND *PHACOPS IOWENSIS* DELO, 1935

Phacops AND RELATED GENERA are morphologically quite uniform. Campbell (1967, p. 33-35) has recently presented a full diagnosis of the genus *Phacops* which will not be repeated here. There is as yet little agreement on reliable, species-specific characters that may be used systematically to clarify the definitions of, and interrelationships among, the many species of *Phacops* described in the literature. Although it is unwise to extrapolate the findings of a single study on but two species and apply a priori the species-specific criteria found to differentiate *P. rana* from *P. iowensis* to the analysis of other species of *Phacops*, certain of these differentia do seem to have importance within the genus as a whole and promise to help untangle the difficult problem of species relationships within *Phacops* and closely allied genera in the Silurian and Devonian.

Foremost among these characters is the eye complex, particularly the distribution of lenses on the visual surface. Steininger (1831, l. 351, ff.) prophetically saw the importance of lens arrangement as an important taxonomic feature of the phacopids, but it was not until Clarkson (1966a, 1966b) presented lens number counts in terms of *dorsoventral files* (see Appendix 1 for a glossary of morphological terms) that the systematic value of lens arrangement within the Phacopidae became clear. Very simply, a unique number of dorsoventral files is reached early in holaspid ontogeny within any single population sample and is stabilized throughout the remainder of ontogeny. With but few exceptions known to me, all variation in dorsoventral file number is interpopulational or interspecific. Variation in total number of lenses in the eye, on the other hand, is a function both of dorsoventral file number and the number of lenses per dorsoventral file. This latter factor is complex and is discussed at length elsewhere (Eldredge, ms); variability in number of lenses per dorsoventral file ranges from asymmetry within an individual through the interspecific level.

Differences in dorsoventral file number form the primary, but by no means the only, means

of distinguishing *P. rana* from *P. iowensis*. In addition, as discussed in detail below, the same criterion is of utmost importance in the delineation of subtaxa within the *P. rana* group. Since Clarkson's (1966a, 1966b) work appeared, the importance of dorsoventral file number in phacopid (*sensu lato*) systematics has been independently discovered by Burton (working on some European species of *Phacops*) and Young (working on American pterygomotopids). There can be no question of the great potential that this easily observed character may have in clarifying the interrelationships among phacopid taxa.

The lenses are always arranged in 13 dorsoventral files (vertical columns) on the visual surface of the eye in all but the smallest postlarval instars of *P. iowensis*. *Phacops rana*, on the other hand, has from 15 to 18 dorsoventral files, and two intermediate populations are known where variation between two or more dorsoventral file numbers is continuous.

Phacops iowensis also tends to have fewer lenses per dorsoventral file than does *P. rana*, and the combination of fewer dorsoventral files and fewer lenses per dorsoventral file amounts to differences in average number of lenses per eye between the two species. The average number of lenses per population ranges from 40 to 48 in different populations of *P. iowensis*, and the maximum number of lenses observed in an individual specimen is 54. Intropopulational variation in average number of lenses is great in *P. rana*, and ranges from a low of 51 to over 100.

In addition to dorsoventral file numbers, other characters serve to differentiate *P. rana* from *P. iowensis*, and, equally as important, to unite as a whole the various populations of *P. rana* with different numbers of dorsoventral files (see figs. 3, 4, 13-16, 22, 23). The librigenal and fixigenal moieties of the ocular platform are far more sharply defined in *P. iowensis* than in *P. rana* because of the more deeply emplaced facial suture in the former.

The exoskeleton of both species tends to be covered by tubercles over wide areas. Tubercles

in *P. iowensis* tend to be of uniform size and are generally rounded at the base, rising in a conical fashion and often terminating in a point. *Phacops rana* shows greater variation in tubercle size and shape, but the tubercles are usually bluntly rounded on top.

Tubercle shape is of critical importance on certain areas of the exoskeleton. In *P. rana*, the tubercles of the occipital lobe and axial rings of the thorax and pygidium become transversely elongated and flattened. Tubercle elongation is also present on the cephalic margin on the genae and particularly on the anterior portion of the composite glabellar lobe, where the elongation is frequently so highly developed as to produce long, wavy transverse ridges similar to those on the external surface of the doublure and hypostoma. No transverse elongation of tubercles is found in *P. iowensis*.

Tubercles in both species tend to be larger on the glabella (including glabellar lobe 1p) than elsewhere on the cephalon. The ocular platform is usually more heavily tuberculated in *P. iowensis* than in *P. rana*.

Tuberculation is generally heavier over the thorax and pygidium in *P. iowensis* than in most populations of *P. rana*. The lateral and posterior margins of the pygidium are heavily tuberculated in *P. iowensis*, and tuberculation is generally obsolescent on the pygidial margins of *P. rana*.

Many specimens of *P. iowensis*, including the holotype (SUI 9-266, see fig. 3), show obsolescence of the 1p glabellar furrow mesially and a consequent tendency toward incorporation of glabellar lobe 1p with the composite glabellar lobe. Whereas other specimens of *P. iowensis* show moderately deep emplacement of glabellar furrow 1p, *P. rana* never shows any obsolescence of this furrow. Glabellar furrows 2p and 3p are variably developed in both species, but perhaps more commonly encountered in *P. iowensis*.

The genal angle terminates in a moderately sharp point in *P. iowensis*, and is somewhat more bluntly rounded in all but the earliest populations of *P. rana*. When the cephalon is oriented with the dorsal margin of the visual surface in the horizontal plane, the genal angle forms the ventralmost portion of the cephalic margin in *rana*. In *iowensis*, with the exception of some of the earlier specimens known, the ventralmost portion of the cephalon is anterior to the genal angle and is situated below the eye. The ventral

margin is thus slightly recurved posterodorsally anterior to the genal angle in *P. iowensis*.

There is no consistent difference in the number of axial rings or pleura on the pygidia of the two species. The pleura are highly arched and the pleural furrows deeply incised in *P. iowensis*, in contrast to the rather flat pleura and shallow pleural furrows in *P. rana*.

The first anterior interpleural furrow commonly is weakly developed in *P. rana*, particularly in specimens from older formations. The

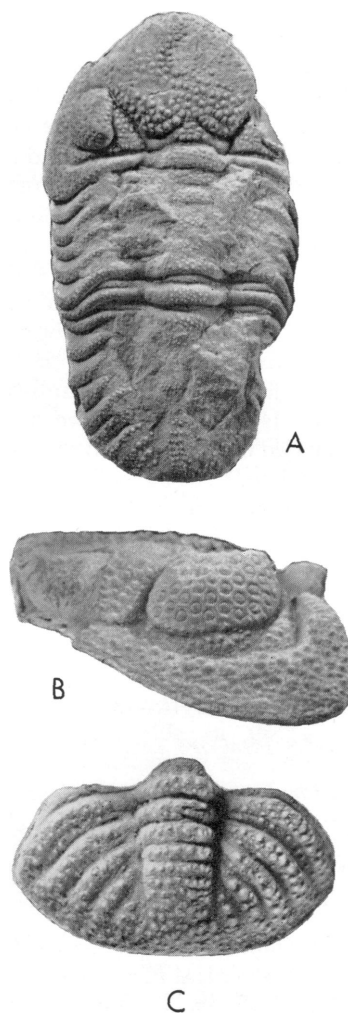


FIG. 3. *Phacops iowensis iowensis* Delo, 1935. A, B. Holotype, Cedar Valley Formation, SUI 9-266. A. Dorsal view, $\times 2$. B. Left lateral view of cephalon, $\times 4$. C. Dorsal view of pygidium, paratype, Cedar Valley Formation, SUI 9-117, $\times 3.5$.

anterior two or even three interpleural furrows are frequently developed in *P. iowensis*.

Additional criteria for distinguishing the two species emerge in factor analysis of linear measurements and are discussed below.

By far the most important differences between the two species are the number of dorsoventral files on the visual surface, shape and distribution of tubercles, particularly on the cephalon, and relative degree of differentiation of the ocular platform into librigenal and fixigenal moieties.

Although the term "biospecies" should perhaps be applied as a conclusion following an exhaustive study, it is perhaps justifiable at this point to claim such status for both *P. rana* and *P. iowensis* as a working hypothesis. The characters enumerated immediately above at the very least justify recognizing both *rana* and *iowensis* as "Operational Taxonomic Units." Full status as "biospecies" further depends upon demonstration of historical cohesion or integrity, which can only be deduced following a full analysis of interrelationships among any subtaxa found to exist, and consideration of geographic and stratigraphic distributional data. But the fact remains that dorsoventral file number and all other characters mentioned above point to the existence of two discrete and internally consistent taxa, and for the purposes of subsequent analysis and discussion, the assumption is made that *P. rana* and *P. iowensis* in fact are true biospecies.

The two species may be diagnosed as follows:

SYSTEMATIC PALEONTOLOGY

FAMILY PHACOPIDAE HAWLE AND CORDA, 1847

GENUS *PHACOPS* EMMRICH, 1839

Phacops iowensis DeLo, 1935

Phacops iowensis DELO, 1935, p. 422-423, pl. 48.

Phacops iowensis: STUMM, 1953, p. 140-142, pl. 12.

Figure 3; see also figures 22, 23

EMENDED DIAGNOSIS: Eyes moderately large, bearing 13 dorsoventral files of lenses in normal adults. Trace of facial suture over ocular platform deeply incised. Genal angles terminating in blunt point, recurved dorsally from ventral cephalic margin. Glabellar furrow 1p variably incised, occasionally obsolescent mesially. Glabellar furrows 2p and 3p weakly

developed or absent. Cephalon covered by round, conical tubercles of uniform size, not becoming elongated transversely.

Thorax generally covered with tubercles similar to those on cephalon.

Pygidium with eight to 10 axial rings and six to eight pleura. Pleura highly arched, pleural furrows deeply incised. Anterior two to five interpleural furrows frequently developed, with area of fused pleuron anterior to interpleural furrow more highly arched than posterior region. Tuberculation heavily developed over

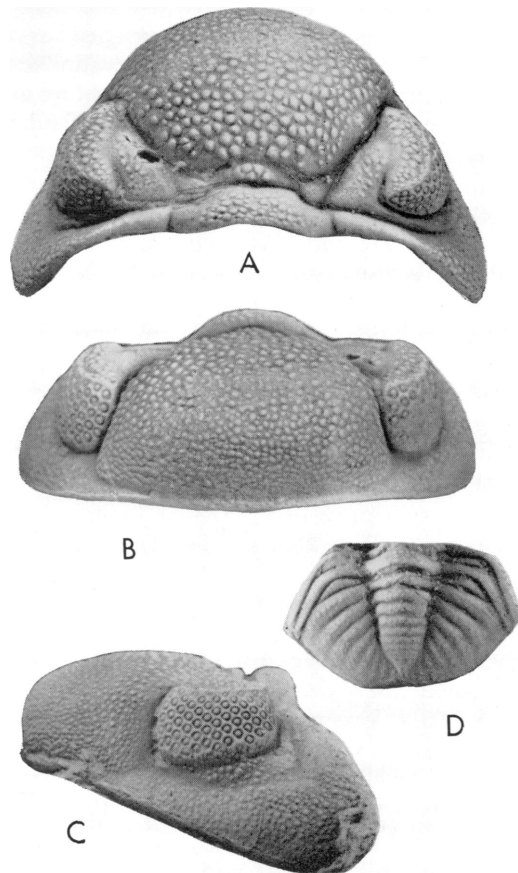


FIG. 4. *Phacops rana rana* (Green, 1832). A, B. Hamilton Group, Eighteen Mile Creek, Erie County, New York, AMNH 5499/1. Figured by Hall and Clarke, 1888, pl. 8, fig. 7. A. Dorsal view of cephalon, $\times 3$. B. Frontal view of cephalon, $\times 3$. C. Left lateral view of cephalon, Hungry Hollow Formation, UMMP locality B, UMMP 24313, $\times 2$. See also figure 24. D. Dorsal view of pygidium, Brandon Substage, Cedar Valley Formation, Belanski collection, SUI 6267, $\times 3$.

entire surface of pygidium, including pygidial margins.

HOLOTYPE: State University of Iowa 9-266.

Phacops rana (Green, 1832)

Calymene bufo var. *rana* GREEN, 1832, p. 42, casts 11, 12.

Calymene bufo: HALL, 1843, p. 201, fig. 80.

Phacops bufo: EMMONS, 1860, p. 138, fig. 124.

Phacops rana: HALL, 1861, p. 55.

Phacops rana: HALL AND CLARKE, 1888, p. 19-26, pls. 7-8.

Phacops rana: DELO, 1940, p. 22-23, pl. 1.

Phacops rana: STUMM, 1953, p. 135-140, pls. 9-12 (in part).

Figure 4; see also figures 13-16

EMENDED DIAGNOSIS: Eyes large, bearing from 15 to 18 dorsoventral files of lenses in normal adults. Trace of facial suture over ocular platform shallow. Genal angles gently rounded and near ventral cephalic margin. Glabella furrow 1p deeply incised, glabellar furrows 2p and 3p weakly developed or absent. Cephalon covered by low, rounded tubercles becoming transversely elongate at the anterior margin of the glabella, on the genae, and on the occipital lobe. Tubercles largest on central region of composite glabellar lobe and glabellar lobe 1p.

Axis of thorax covered with transversely elongate tubercles. Tuberculation on pleura variably developed.

Pygidium with from seven to 10 axial rings and six or seven pleura. Tubercles moderately elongate transversely on axis; tubercles cover pleura, becoming obsolescent on pygidial margin. Interpleural furrows generally obsolescent, anteriormost interpleural furrow occasionally present as shallow groove set off by parallel rows of tubercles. Pleural furrows rather shallow, pleura only moderately arched.

HOLOTYPE: NYSM 13887/1.

THE AFFINITIES OF *PHACOPS RANA* AND *PHACOPS IOWENSIS*

Hall and Clarke (1888, p. 24) observed that *P. rana* seemed more closely related to species of *Phacops* from Germany than to any other species found in the Devonian of North America. Examination of specimens of Lower and Lower Middle Devonian species of *Phacops* in the collections of the American Museum of Natural History and the Museum of Comparative Zoology, Harvard University, strongly confirms the opinion of Hall and Clarke.

Gedinnian-Siegenian species of *Phacops* currently recognized from North America include *P. logani* Hall, 1861, *P. hudsonicus* Hall, 1861, *P. raymondi* Delo, 1935, and *P. claviger* Haas, 1969. Emsian-Eifelian species include *P. cristata* Hall, and *P. cristata* var. *pipa* Hall and Clarke, 1888, as well as variants of *P. cristata* recently described by Stumm (1954). Each of these species is characterized by tuberculation essentially identical in shape and distribution to the condition in *P. iowensis* described above. In addition, *P. logani* has 17 dorsoventral files, whereas *P. hudsonicus* has probably 16 files, and *P. raymondi* has 15. *Phacops cristata* and *P. cristata* var. *pipa* each have 14 dorsoventral files. It seems quite probable that these species are closely related and that there is a definite character gradient involving reduction in number of dorsoventral files throughout the Lower and Lower Middle Devonian. *Phacops iowensis* with 13 dorsoventral files also belongs to this "Native North American" species complex. In most other aspects of morphology, *P. iowensis* is very similar to *P. cristata* var. *pipa*. In addition, a single specimen in the collections of the National Museum of Natural History (USNM 78923) from the Gedinnian Linden Formation of Tennessee with 13 dorsoventral files is surprisingly similar in all respects to specimens of *P. iowensis* from the Hungry Hollow Formation of Ontario. *Phacops iowensis* was almost certainly derived from a native North American Devonian species.

Among well-known species, the closest relative to *P. rana* seems to have been *P. schlotheimi* (Bronn) from the Eifelian of Germany and elsewhere. Details of genal angle and ocular platform morphology, and mode of tuberculation are closely comparable in the two species. Furthermore, *P. schlotheimi* has 18 dorsoventral files and a 15 file variant, and the 18 dorsoventral file specimens can be further subdivided into two eye variants (Burton, MS.a, MS.b). This situation closely resembles the pattern of variation seen in the earliest (Cazenovian) populations of *Phacops rana* as discussed below. In addition, *P. rana* has recently been found to occur in certain areas of the Spanish Sahara of northwest Africa (Burton and Eldredge, MS).

If *Phacops rana* or its immediate ancestor did migrate from the Devonian European or North African areas to Devonian North America, it was not the only trilobite to do so. *Greenops*

(*Greenops*) *boothi* (Green, 1837) is a native dalmanitacean of the predominantly European subfamily Asteropyginae. This subfamily ranges from Lower Devonian into the Upper Devonian in Europe, but is represented in North America by the single subgenus *Greenops* (*Greenops*) found in Cazenovian, Tioughniogan, and Taghanic rocks (Stumm, 1954, p. 202). Its earliest unquestionable occurrence is in the Solsville member of the Marcellus Formation (AMNH loc. 3013) slightly higher stratigraphically than the earliest known occurrence of *P. rana*. As it is evident that there were marine connections between Europe-Africa and North America in upper Eifelian or lower Givetian times suitable for the migration of *Greenops* to North America, it is conceivable that species of *Phacops* may also have come in from the European-northwest Africa faunal province. In view of the striking similarity between *P. rana* and European-African species of *Phacops*, and the great discrepancies between *P. rana* and species of *Phacops* found in the Lower and Lower Middle Devonian of North America, a European-African ancestry for *Phacops rana* seems well founded.

PREVIOUS WORK ON MIDDLE DEVONIAN PHACOPID TAXA IN NORTH AMERICA

Although *Phacops* has attracted much attention in paleontological and biostratigraphic research in the Middle Devonian of North America, there exist only a relatively few comprehensive studies of the systematics of these trilobites.

Hall and Clarke (1888, p. 19-26) gave a detailed description and discussion of *P. rana* that remains the most complete and generally excellent treatment of the anatomy of this trilobite to be found in the literature. However, they accorded little recognition to variation in specimens from outside New York State, and knowledge of regional Middle Devonian stratigraphy was probably insufficient to allow recognition of variation through time. In addition to *P. rana*, Hall and Clarke recognized *P.*

nupera Hall from the Chemung sandstone and *P. cacapona* Hall from the Hamilton of Virginia as probably valid.

Stewart (1927, p. 58) recognized a new "variety" of *P. rana*, *P. rana* var. *milleri* from the Silica shale of Ohio. The new variety was based largely on details of lens number and morphology of the visual surface.

Delo (1935, p. 422-423) recognized a new species, *P. iowensis*, from the Cedar Valley of Iowa. In a later paper (1940, p. 22-23), Delo indicated that not all *Phacops* from the Traverse Group of Michigan, the Milwaukee Formation, and the Devonian of Virginia were conspecific with *P. rana sensu stricto*, though he recognized no new taxa. In addition, Delo (1940, p. 21) correctly considered *P. nupera* as unrecognizable and probably referable to *P. rana*. Delo (1940, p. 16) also correctly regarded the cotypes of *P. cacapona* as a mixture of true *P. rana* and *P. cristata* var. *pipa* Hall and Clarke.

Stumm (1953) reviewed the systematics of *Phacops* from the Traverse Group of Michigan and the Devonian of northwestern and north-central Ohio, and southwestern Ontario. He recognized seven subspecies of *P. rana* and two subspecies of *P. iowensis* from these beds. Criteria of differentiation of these taxa primarily involved differences in total lens number in relation to cephalic size, number of lenses per "vertical row," mode of ornamental tuberculation, and gross proportional differences evaluated qualitatively.

Finally, Stumm (1954) described *Phacops ohioensis* on the basis of two pygidia from the Dundee limestone of Michigan and Ohio. These pygidia are probably not phacopid, and seem closely comparable to the pygidium of a species of the proetid genus *Dechenella* in the Jeffersonville limestone of southern Indiana (Stumm, 1964b).

It may be concluded, then, that *P. rana* and *P. iowensis* are the only recognizable taxa correctly referred to *Phacops* in the span of Middle Devonian time in North America under consideration here.

ANALYTICAL TECHNIQUES

REPEATABILITY AND BIOLOGICAL interpretability of measurements on any organism depend to a large degree on the manner of orientation of the specimen. Clarkson (1966c), in his discussion of "*Phacops*" *musheni* Salter, argued that the most likely orientation of the cephalon in life was with the dorsal margin of the visual surface in the horizontal plane. This conclusion is based on Clarkson's studies on the physiological implications of lens arrangement in *P. musheni*, and seems to be applicable to phacopids in general; this orientation was consequently adopted for all cephalic measurements on *P. rana* and *P. iowensis*.

Each specimen was mounted with Plasteline on a square wooden block with the dorsal margins of both visual surfaces in the same horizontal plane. Thus the dorsal surface of the palpebral lobe was normal to the line of vision. Rotation of the block enabled the specimen to be viewed anteriorly, laterally, or posteriorly in a systematic manner. Pygidia were mounted with the surface of the first axial ring in the horizontal plane.

All measurements were made with an ocular micrometer mounted in the eyepiece of a low-powered, binocular stereoscopic microscope, where 1 millimeter was equal to 7.4 micrometer units. Angles were measured with a goniometer attached to the microscope.

Shaw (1957, p. 193) has discussed the problem of comparing measurements made on trilobites with the exoskeleton intact with those on exfoliated specimens. His conclusion, that the measurements are usually quite comparable if made to the deepest part of bounding furrows, seems sound and has been followed here, although preference was given to nonexfoliated specimens.

The measurements are described in table 1 and illustrated (cephalon only) in figure 5. As most of the measurements involve simple linear dimensions of clearly defined anatomical parts, they need not be discussed further.

The terms "sample" and "population" are used nearly interchangeably herein. Most of the collections used, particularly for measuring purposes, come from a single locality and in most cases from a very short stratigraphic

interval; ideally this interval would be a single bedding plane, but few collections available came from such a short interval. The term "population" is thus extended here to include all specimens collected within a short interval of rock representing an interval of time far shorter than the most abbreviated of time stratigraphic or biostratigraphic units regionally recognizable in the Middle Devonian of North America.

The general family of multivariate clustering techniques known as factor analysis has been shown to have a wide range of applicability to paleontological problems (Eldredge, 1968). Various forms of factor analysis have proved useful in this study in the clarification of character gradients, discrimination between *P. rana* and *P. iowensis*, and the study of interrelationships among variables during the ontogeny of a population sample of *P. rana*.

Factor analysis is essentially the resolution of an $N \times n$ data matrix Z into an $N \times m$ factor coefficient matrix A and an $m \times n$ factor components matrix F , where N is the number of samples (specimens here), n is the number of variables, and m is the rank of the data matrix, equal to the number of mutually perpendicular theoretical vectors needed to explain a chosen percentage of the variance of the data matrix. The basic equation is thus $Z = AF$. The aim of factor analysis is to reduce the dimensionality of the data space from n , the number of variables or original reference vectors, to m , which is hopefully much smaller than n . The first theoretical vector represents the axis of major variation of the original data swarm, and the following vectors represent successively minor directions of variation. A further step, where the calculated factor axes may be rotated to achieve a better fit to the data swarm, may be carried out by a best-fit procedure such as the Varimax criterion. Thus, each specimen (N_i) will have a score or coefficient on each factor, and each variable (n_j) will have a certain score, or relative importance, in the composition of each factor. This general series of procedures has been referred to as "Q-mode" factor analysis.

"R-mode" factor analysis simply factors a transposed data matrix Z' , so that the factor

TABLE 1
MEASUREMENTS OF THE CEPHALON AND PYGIDIUM

CEPHALON	
TCL	Total cephalic length, sagittally from front of glabella to transverse line joining posterior margins of genal angles
CL	Cephalic length, sagittally from front of glabella to rear of occipital lobe
GL 1p	Length of composite glabellar lobe, sagittally from front of glabella to glabellar furrow 1p
1pL	Sagittal length of glabellar lobe 1p
OCL	Sagittal length of occipital lobe
PEG	Distance from anterior margin of visual surface to anterior (sag.) margin of cephalon
LVS	Maximum length of visual surface
LLVS	Anterior length of visual surface, from anterior margin to palpebral line
LPA	Length of palpebral area, from occipital furrow to intersection of axial and palpebral furrows
L	Distance from palpebral line to posterior margin (sag.) of occipital lobe
LOP	Length of ocular platform from posterior margin of visual surface to occipital furrow
MI1pA	Distance between proximal margins of 1p apodemal invaginations
M1pA	Distance between distal margins of 1p apodemal invaginations
OMIA	Distance between proximal margins of occipital furrow apodemal invaginations
OMA	Distance between distal margins of occipital furrow apodemal invaginations
MIGW	Glabellar width immediately anterior to glabellar furrow 1p
CW	Maximum cephalic width just anterior to posterior margins of genal angles
WBVS	Width between visual surfaces along palpebral line
GWCM	Glabellar width where axial furrows intersect anterior cephalic margins
GWE	Glabellar width where dorsal portion of visual surface intersects axial furrow
WVS	Width of visual surface along palpebral line
WPA	Width of palpebral area along palpebral line
WPL	Width of palpebral lobe along palpebral line
WPAO	Width of palpebral area along occipital furrow
1pW	Width of glabellar lobe 1p
CW1p	Width of 1p glabellar lobe, exclusive of distal nodes
WOC	Width of occipital lobe
WOP	Width of ocular platform from axial furrow to distal margin
HGL	Anterior height of glabella (sag.)
FARCH	Height of frontal arch, from anterior ventral margin to line connecting genal angles (sag.)
ARCH A	Angle of line connecting anterior margin of cephalon to lowest margin of the genae, from the horizontal
HVS	Height of visual surface along palpebral line
HEYE	Total eye height, from top of visual surface to cheek, including ocular platform if distinguishable from cheek
COUNTS MADE ON CEPHALON	
No. TPL	Number of tubercles on palpebral lobe
No. TPA	Number of tubercles on palpebral area
No. TOR	Number of tubercles on occipital ring
No. T1p	Number of tubercles on glabellar lobe 1p
No. TFC	Number of tubercles on fixigena, including ocular platform
No. TSL	Tubercles on sagittal line of composite glabellar lobe
No. TTL	Tubercles on composite glabellar lobe along transverse line at anterior margins of the visual surface
No. COL	Number of dorsoventral files of lenses/eye
Eye Count	Number of lenses/dorsoventral file written in groups of three starting with most anterior dorso-ventral file number 1
Total number of lenses – Summation of eye count formula	
MEASUREMENTS MADE ON PYGIDIUM	
TLPYG	Total sagittal length, from ring furrow of anterior segment to posterior margin of pygidium
LPAX	Length (sag.) from ring furrow of anterior segment to posterior margin of axis
MLPYG	Length (sag.) from line connecting anterolateral pygidial margins to posterior margin
WAPYG	Width between anterolateral margins

TABLE 1—(Continued)

W5P	Total width at level of axial segment 5
L $\frac{1}{2}$ R	Length (sag.) of articulating half-ring
W $\frac{1}{2}$ R	Width of articulating half-ring
LS1, LS5	Length (sag.) of axial segments 1 and 5
WS1, WS5	Width of axial segments 1 and 5
WPLF	Width of pleural furrow of anterior pleuron
COUNTS MADE ON PYGIDIUM	
No. PYG	Number of axial segments
No. PL	Number of pleura
MEASUREMENTS MADE ON THORACIC SEGMENTS	
LTS 1, 6, 11	Length (sag.) of segments 1, 6, and 11
WTS 1, 6, 11	Width of segments 1, 6, and 11
WPLF 1, 6, 11	Width of pleural furrow of segments 1, 6, and 11
WTPL 1, 6, 11	Total width of segments 1, 6, and 11

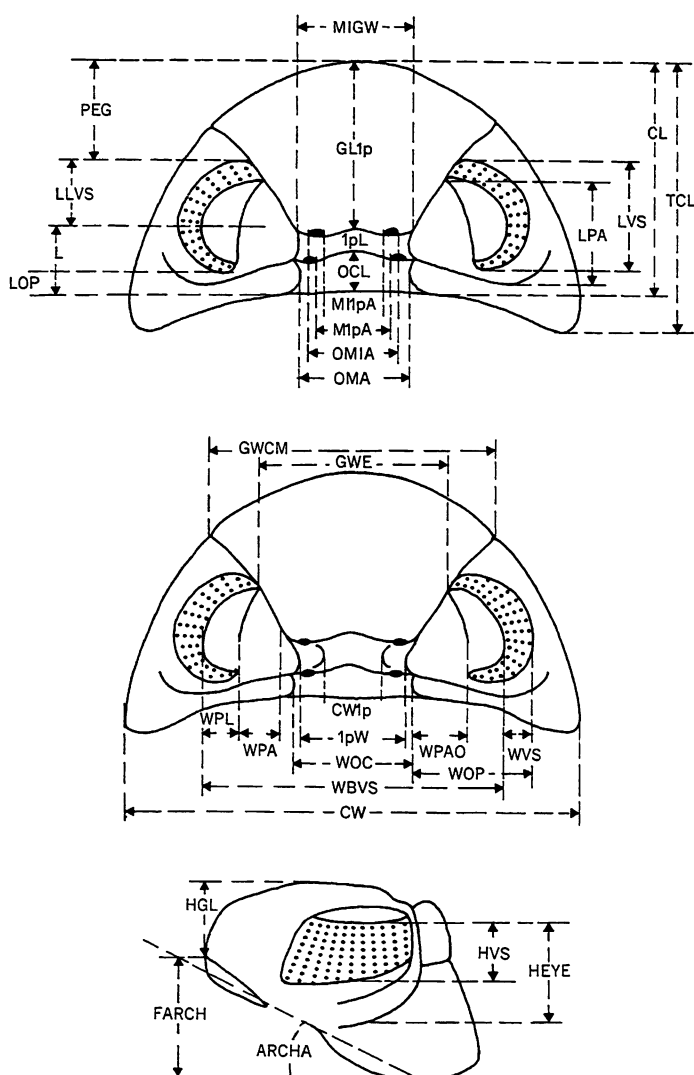


FIG. 5. Cephalic measurements. See table 1 for abbreviations.

coefficients matrix (A) consists of the scores of each variable on the m factors and the factor components matrix (F) reflects the relative contribution of each specimen to each of the m factors. R-mode factor analysis is useful in the study of the interrelationships of variables and gives results comparable to those of the "morphological integration" procedure given by Olson and Miller (1958).

Transformation of the original data matrix before factoring is frequently useful to clarify relationships between samples or between variables. For example, conversion to logarithms is useful in removing allometric effects. Three such data transformations are used here. In analysis of sample interrelationships ("Q-mode"), it is often convenient to make all the sample vectors equal in length. The sum of the squared elements of a vector is equal to the variance or total information of the vector, and it is further convenient to give each specimen a variance equal to unity. This "normalization by cases" is accomplished by dividing each original observation on a specimen by the square root of the sum of the squared observations on that specimen.

An alternative transformation is normalization by variables, which gives each of the n variables a variance equal to one. Normalization by variables is of course accomplished in the same way as is normalization by cases, except that each element in a column vector is

divided by the square root of the sum of the squared observations. The effects of these two transformations on the results are discussed in conjunction with the actual analyses presented below.

In R-type analysis, each observation is subtracted from the mean and the data is then normalized by variables, so that $Z'Z$ becomes the familiar correlation coefficient matrix.

The factor analyses were performed on a CDC 6600 computer operated by the CEIR corporation. Programs included MUST, a multifaceted factor analysis package developed by V. Manson; MUST includes COVAP, an earlier program developed by Manson and Imbrie (1964) used here for R-mode analysis.

A multiple regression program developed by the IBM corporation for the IBM 360 computer as part of their Scientific Subroutine package was run on an IBM 360-50/75 system at Columbia University. Multiple regression is similar in all its essentials to standard bivariate regression analysis, except that a hyperplane in multivariate space is fitted to the data swarm instead of the conventional straight line. However, the object is still to predict one "dependent" variable by one or more predictor, "independent" variables, and the application of this technique to the study of ontogeny is basically the same as it is in standard bivariate regression analysis.

ONTOGENY OF THE CEPHALON OF *PHACOPS RANA*

INTRODUCTION

THE ONTOGENY of trilobites may be conveniently divided into three periods. The *protaspis* is characterized by a larval cephalon directly articulated with a protopygidium. In the *meraspis* period, thoracic segments are added progressively until the adult number is reached; any individual with the adult number of thoracic segments belongs to the *holaspis* period (see Whittington, 1957, 1959, for recent reviews of trilobite ontogeny).

Analysis of ontogeny and statistical comparisons of populations of *Phacops* are limited to the *holaspis* period in the present study. Minute specimens probably referable to the *protaspis* period of *P. rana* are occasionally found, but are far too rare to enter into statistical analysis. Lack of complete specimens where the number of thoracic segments is known precludes accurate separation of late *meraspis* "degrees" from early *holaspis* instars.

As in other arthropods, growth continues in the postlarval (*holaspis*) stage. Since ontogenetic size increase proceeds in discrete molt stages, postlarval ontogeny of fossil arthropods must be studied on the population level by collection of suites of specimens of different sizes. Thus the ontogenetic record of an individual is lost, or at least unrecognizable, and generalizations on ontogenetic processes are based on over-all population tendencies. Fossil arthropods therefore occupy a somewhat intermediate position between some groups (e.g., molluscs) in which individuals retain a continuous record of the ontogeny of hard parts, and other groups (e.g., vertebrates) in which only the latest stage of ontogeny is generally observable in any one specimen (Gould, 1966). The ontogeny of fossil vertebrates must be studied on the basis of a suite of specimens arranged according to size, but as smaller specimens, particularly of terrestrial species, commonly represent unsuccessful individuals that died before reaching full adult size, population ontogenetic analyses of fossil vertebrates are probably less truly representative of the actual ontogenetic process than are analyses based on molt series of fossil arthropods.

The general mode of growth in *Phacops* is sufficiently simple so that ignorance of the ontogeny of individual specimens is not a serious problem. However, inability to distinguish the "trajectory" of the ontogeny of an individual within the data swarm creates serious difficulties in studies of the development of the lenses on the visual surface of the eye. Ontogeny of the visual surface is discussed in the present paper only in conjunction with systematic problems.

SOME GENERAL CONSIDERATIONS

Ontogenetic allometry, in its broadest sense, is any change in proportion during development (Gould, 1966). Thus allometry may occur even though growth may be described by the simple equation for a straight line, $y=ax+b$, where a is the slope and b the intercept of the line. If b is significantly different from zero, the proportion between any two variables being compared will change as growth occurs. As Shaw (1956) has shown, the widespread use of ratios in the systematic literature of trilobites is undesirable as these ratios may change in ontogeny. Ratios are of course useful if comparable molt stages can be identified, although in practice the identification of discrete molts is difficult. Comparison of ratios between two or more populations may also be appropriate if specimens of comparable size are used, although the possibility of phylogenetic or even geographically based size increase or decrease may invalidate the results.

It is by now apparent that, in terms of linear dimensions of the exoskeleton, *holaspis* growth in trilobites may usually be described by a simple linear equation. The power function, $y=bx^k$, commonly applied to both ontogenetic and phylogenetic cases of allometry, is generally unnecessary to describe growth within the *holaspis* period. Hunt's (1967) work on the agnostid *Trinodus elspethi* (Raymond) from the Ordovician Edinburgh Formation, Saul's (1967) and the author's unpublished data on homalonotids, Bright's (1959) study of the ontogeny of the ptychopariid *Elrathia kingii* (Meek), Pabian and Fagerstrom's (1968) work on *Ameura sangamonensis* (Meek and Worthen) and Whit-

tington's (1957) analysis of *Isotelus gigas* DeKay are but a few examples where linear equations are adequate to describe holaspid growth. In addition, Waterman (1954) has shown that in terms of the major dimensions of both the prosoma and opisthosoma of *Limulus polyphemus* (L.) and *Tachypleus tridentatus* Leach, postlarval growth in the Xiphosura is not only linear, but essentially isometric.

The degree of allometry present in holaspid ontogeny must be understood before comparisons between populations are made, as samples from different areas and formations commonly represent different segments of ontogeny. Such sampling biases could easily lead to spurious results if allometry is a significant factor in the postlarval growth of a tagma. Although Giles (1960, p. 373) claimed that allometric effects would be negligible in interpopulational comparison of coyote samples, and that "testing for allometry would be a study in itself," certainly some degree of testing is necessary before results of statistical discrimination between populations are accepted.

QUALITATIVE HOLASPID ONTOGENY OF *P. rana*

No consistent changes in the ontogeny of ornamentation and other qualitative features were noted in either *P. rana* or *P. iowensis*. As Hall and Clarke (1888, p. 23) pointed out, the smallest *P. rana* specimens are in most respects miniature adults.

PLOTTING AND BIVARIATE ANALYSIS

Bivariate plotting and regression analysis show that cephalic growth in *P. rana* is linear and closely conforms to patterns seen in other trilobites. With the exception of certain linear dimensions of the eye, bivariate scattergrams show a very tight unimodal distribution. A single example, based on data on the *crassituberculata* eye variant from the Silica shale ("SILC": UMMP loc. E), where cephalic length (CL) is plotted against the major reliable width measurement (WBVS) is shown in figure 6. The reduced major axis (Imbrie, 1956, p. 234) has an intercept of 1.45 units (=0.2 mm.), indicating that the proportion of CL to WBVS undergoes little change. Schwimmer (MS) has come to a similar conclusion as a result of his study of *P. rana* from the Wanakah shale of western New York.

MULTIPLE REGRESSION

Multiple regression analyses of the same population (SILC) of cephalic length (CL) versus one set of 13 gross cephalic measurements (predictors) and another set of measurements of the eye complex are summarized in tables 2 and 3. Absolute values of the standard partial regression coefficients (beta weights) for the predictors indicate the relative contributions of the corresponding variables to the prediction of the criterion (CL). R^2 is an estimate of the total variance of the criterion explained

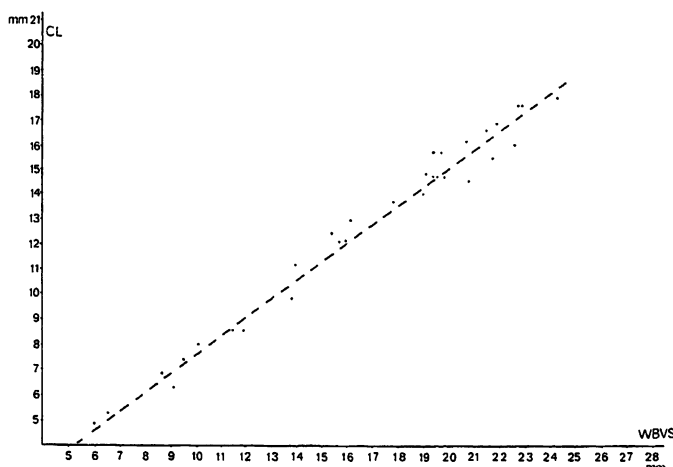


FIG. 6. Bivariate scattergram of cephalic length (CL, ordinate) vs. width between visual surfaces (WBVS, abscissa). *Phacops rana crassituberculata*, Silica shale, UMMP locality E. Reduced major axis shown by dashed line: $CL = 0.75WBVS + 1.45$, in original micrometer units, where 1.45 units = 0.2 mm. $N = 36$.

TABLE 2
MULTIPLE REGRESSION OF 13 GROSS CEPHALIC
DIMENSIONS (PREDICTORS) AGAINST CEPHALIC LENGTH
(CRITERION)^a

Variable	Beta Weight
GLIP	0.72
IPL	0.15
OCL	0.18
GWCM	-0.05
GWE	-0.02
MIGW	0.08
IPW	-0.03
GWIP	0.00
MIIPA	-0.01
MIPA	0.02
OMIA	0.01
OMA	0.02
WOC	-0.04
R ²	0.99908
Intercept	0.45013 units=0.06 mm.
p	<0.01

^a*P. rana crassituberculata* (SILC) only (UMMP loc. E).
N=30.

Symbols: as in table 1.

TABLE 3
MULTIPLE REGRESSION OF 13 VARIABLES OF THE EYE
COMPLEX (PREDICTORS) AGAINST CEPHALIC LENGTH
(CRITERION)^a

Variable	Beta Weight
WVS	-0.02
WPL	0.18
LPA	0.02
WPAO	-0.16
WPA	0.16
WBVS	-0.23
WOP	0.25
L	0.37
HVS	0.12
HEYE	-0.03
LVS	0.06
LLVS	0.20
PEG	0.13
R ²	0.99736
Intercept	0.93036 units=0.13 mm.
p	<0.01

^a*P. rana crassituberculata* (SILC) only. N=30.
Symbols: as in table 1.

by the predictors, and its statistical significance is also included in the tables.

As is shown in table 2, 99.91 per cent of the variance in CL is explained by the 13 gross cephalic measurements. It is hardly surprising that glabellar lengths, rather than widths, are better predictors of cephalic length. What is of interest here is that the hyperplane has an intercept of +0.45 units, equal to 0.06 mm. In terms of glabellar lengths, at least, there is apparently no significant allometry in relation to total cephalic length. Axial widths are relatively poor predictors of CL; although it may be suspected that this is owing simply to the masking effects of glabellar lengths, allometry of axial widths in relation to cephalic length cannot be ruled out entirely on the basis of this analysis.

The various linear measurements of the eye explain 99.74 per cent of the variance of CL, and the intercept is 0.93 units, or 0.13 mm. (table 3). There is a more even contribution of the variables to the prediction of CL, probably reflecting the more homogeneous size range of the variables. There seems to have been little significant allometry between the entire eye complex and cephalic length.

FACTOR ANALYSIS

R-type factor analysis of the same population (SILC) clusters variables in terms of specimens. The first factor extracted shows a tight grouping of most of the variables and is basically a simple growth factor. Two other factors extracted yield more interesting results in rotated solution. When factors 2 and 3 are plotted against factor 1, (figs. 7, 8) a very tight cluster of main cephalic width and length measurements is apparent. However, measurements of the eye can be discriminated from the main cluster by all three factors. The close association of gross measurements, including axial widths, along all three factors, is a strong indication that allometry is insignificant in the ontogeny of the glabella and over-all cephalic dimensions. Although multiple regression indicated little allometry between the eye complex as a whole and cephalic length, it does appear that the eye complex maintains a measure of independence from the axial portion of the cephalon during ontogeny. Interrelationships of variables within the eye complex are discussed in a forthcoming paper (Eldredge, ms).

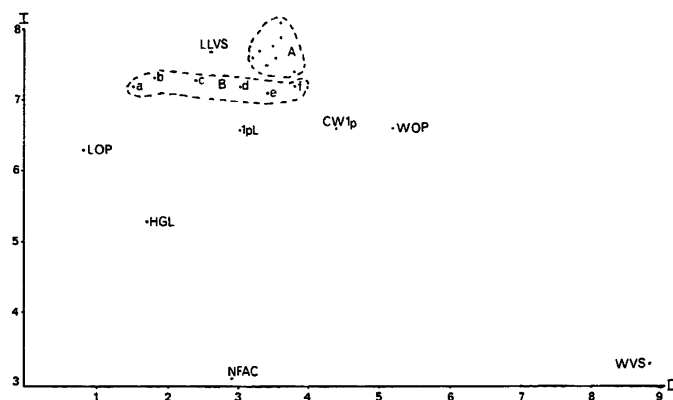


FIG. 7. R-mode factor analysis (rotated solution) plot of factor I (ordinate) vs. factor II (abscissa) for *P. rana crassituberculata* cephalae, Silica shale, UMMP locality E. $N=28$. Two groups, A and B, are outlined by dashed lines: Group A consists of major linear dimensions of the cephalic axial structures; Group B: a—HVS; b—HEYE; c—WPA; d—LPA; e—WPAO; f—WPL. Other abbreviations as in table 1.

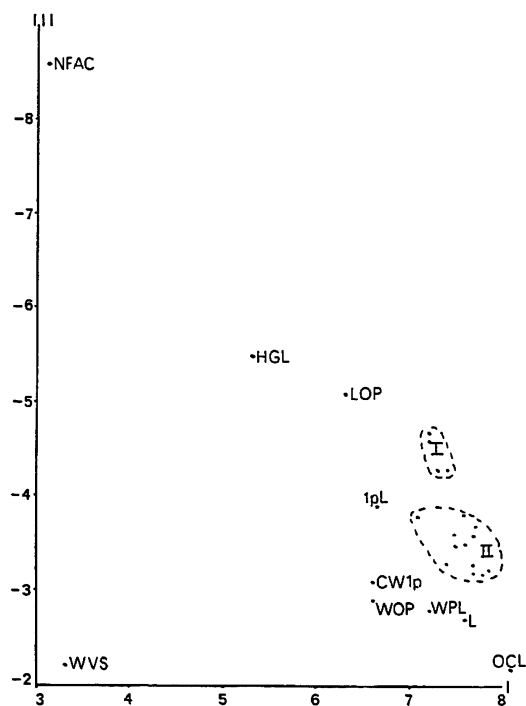


FIG. 8. R-mode factor analysis (rotated solution) plot of Factor III (ordinate) vs. Factor I (abscissa) for *P. rana crassituberculata* cephalae, Silica shale, UMMP locality E. $N=28$. Two groups, I and II, are outlined by dashed lines. Group I consists of HVS, LPA, HEYE, and WPA; Group II consists of major cephalic dimensions. Other abbreviations as in table 1.

Several variables show rather high independence. For example, factor 2 seems to measure diagenetic deformation. The width of the visual surface (WVS) and width of the ocular platform (WOP) could easily have been distorted by deformation of the genae, structurally the weakest portion of the cephalon. Measurements made proximal to the distal margin of the palpebral lobe seem far less prone to variation induced by deformation. A few variables (e.g., MIIPA, MIPA) are omitted because of incorrect results caused by errors in the original data matrix.

CONCLUSIONS

Postlarval growth in *Phacops*, as in other trilobites and living xiphosurans, is linear and can be adequately described by the equation for a straight line. Furthermore, allometry, while present between certain variables, is generally sufficiently negligible that populations may be compared even when biased in terms of portions of the ontogenetic sequence represented.

The cephalon is basically well "integrated," reflecting its nature as a solid tagma. The ocular complex, however, maintains a degree of independence from the major cluster of gross and axial dimensions.

INTERPOPULATIONAL VARIATION IN *PHACOPS RANA*

THE VERY CHARACTERS that may be used to differentiate *P. rana* from *P. iowensis* are the ones that show the greatest amount of interpopulational variation within the *P. rana* complex as a whole. This fact suggests a significant amount of interaction between the two species, and that consequently their histories cannot properly be understood separately. The details of the apparent interactions between these two species are discussed following a general discussion of interpopulational variation within each of the species.

The interspecific differentia discussed previously included aspects of the eye complex (particularly number of dorsoventral files), shape and distribution of ornamental tubercles, genal angle morphology, and pygidial characters. In addition size and shape differences of various anatomical areas of the exoskeleton which emerged in factor analysis may be added.

ORNAMENTATION

On the cephalon of *P. rana* the low, rounded tubercles become elongated transversely, often into ridges, on the occipital lobe, genae, and particularly on the anterior margin of the composite glabellar lobe. This elongation into ridges is progressive, so that at the cephalic margins, the ridges are similar to those on the doublure and hypostoma.

Within the *P. rana* complex, there is a spectrum ranging from a strong development of flattened and elongated tubercles, to a virtual absence of this feature. In Cazenovian samples, flattening and elongation of the tubercles begins on the horizontal posterior surface of the composite glabellar lobe, and increases in intensity anteriorly down the frontal slope to the anterior cephalic margin. Virtually all but the most anterior tubercles on the occipital lobe are similarly transversely elongate. This state is most extremely developed in the populations of the Cazenovian. In Tioughniogan samples, flattening begins farther down the anterior slope of the glabella and is less extreme at the anterior cephalic margin. Although specimens of *P. rana* from the Taghanic (Tully) of New York retain this elongation on the anterior

slope, specimens from the Taghanic of the west (Milwaukee Dolomite, Cedar Valley Formation) show almost complete loss of flattening and elongation, retaining the elongate tubercles only on the anterior margin of the glabella and on the posteriormost row of tubercles on the occipital lobe.

GENAL ANGLE

The genal angle is situated on the ventral lateral margin of the cephalon in lateral view with the dorsal margin of the visual surface in the horizontal plane. In Cazenovian samples of *P. rana* the genal angle is generally quite acute, whereas the genal angles of Tioughniogan and Taghanic samples are generally more rounded.

OCULAR PLATFORM

All Cazenovian samples have shallow facial suture furrows and a relatively flat librigenal moiety. The facial suture furrow is deeper and there is a tendency for the librigenal moiety to become vertical and merge imperceptibly with the area under the visual surface in specimens from the Tioughniogan. This condition is developed to an extreme in specimens of *P. rana* from the Taghanic.

THE PYGIDIUM

The pygidium is a solid tagma that undergoes little postlarval ontogenetic change in qualitative characteristics and there is interpopulational variability in only a few characters.

Large, gently rounded tubercles generally cover the axis and proximal regions of the pleura in Cazenovian *P. rana* and become obsolescent near the margin. Larger specimens of the *milleri* eye variant often show incipient obsolescence over the entire thorax and pygidium. Specimens of *P. rana* from the Taghanic, particularly those from the Cedar Valley and Milwaukee formations, frequently show smaller, more conical tubercles distributed over the entire surface of the pygidium, including the posterior and lateral margins. Strength and distribution of tuberculation is quite variable between populations of *P. rana* throughout the Tioughniogan.

All but the first interpleural furrows are generally obsolescent in *P. rana*. Cazenovian samples, including *P. rana paucituberculata*, in many cases have the anterior interpleural furrow developed as a faint transverse groove, commonly set off by two parallel rows of tubercles. Tioughniogan specimens display the interpleural furrow less frequently, and this feature is generally absent in Taghanic samples. Degree of incision of the pleural furrows and degree of arching of the pleura seem to converge with the interpleural furrow. Shallow furrows and relatively flat pleura characterize most Cazenovian populations. Tioughniogan *P. rana*, again, are variable, but Taghanic samples show deeply incised pleural furrows and more highly arched pleura.

INTERPOPULATIONAL VARIATION IN NUMBER OF DORSOVENTRAL FILES

As in intrapopulational and ontogenetic variability, much of the variation seen on the interpopulational level within *P. rana* involves eye morphology. The number of dorsoventral files per eye is particularly significant. As noted previously, the normal adult complement of dorsoventral files is virtually invariant within a population. Smallest holaspisid cephalons observed have but two or three fewer dorsoventral files than the adult number, and the normal adult complement is quickly reached and stabilized. Variations in dorsoventral file number within some populations are not uncommon but are rarely symmetrical. At least one of the eyes on any specimen is likely to be normal for the population. Only two populations have been encountered that exhibit significant variation in this feature.

The oldest specimens of *P. rana* known occur as rare specimens in the Dundee and Delaware limestones of Ohio and in the Solsville member of the Marcellus Formation in central New York (fig. 13D). They are uniformly characterized by 18 dorsoventral files, a characteristic they share with their European relative, *P. schlotheimi*. *Phacops rana* populations with 18 dorsoventral files persist into the upper Cazenovian Skaneateles equivalents generally west of the exogeosyncline of New York and the Appalachians. They occur in Skaneateles equivalents in Michigan (Bell shale, Rockport Quarry limestone, Ferron Point Formation, Genshaw Formation), Illinois (St. Laurent

limestone), Indiana (Deputy and Silver Creek limestones), Ohio (Silica shale), and southwestern Ontario (Arkona shale). In addition, they are known from float material in Iowa and from lower Hamilton rocks in the southern Appalachians. Two eye variants primarily involving differences in number of lenses per dorsoventral file, have led to recognition of two subtaxa within the 18 dorsoventral file group: *P. rana milleri* Stewart (fig. 14), and *P. rana crassituberculata* Stumm (fig. 13). The number of lenses per dorsoventral file is a component of interpopulational variation not encountered again in the subsequent history of *P. rana*, and the general nature of this geographic variability and the validity of *P. r. crassituberculata* and *P. r. milleri* as distinct subspecies are discussed below.

The ontogeny of the eye of populations with 18 dorsoventral files suggests that the first (anterior) file is added last in ontogeny. This file is reduced to a single lens in the one specimen known from the lower shale of the Solsville member of the Marcellus (AMNH loc. 3013) of New York (fig. 13D). A small sample from the overlying sandstone unit of the Solsville (AMNH loc. 3013) shows great variation in the development of the first file. One specimen has the file fully developed, whereas in others it is partially developed or totally absent. The oldest *Phacops*-bearing unit above the Solsville in New York is the Stafford limestone, which is either uppermost Marcellus or lowermost Skaneateles in age. All *Phacops* from this formation have 17 dorsoventral files, and all 17 file populations of *P. rana* were limited to the eastern exogeosyncline throughout the duration of the Cazenovian. As the holotype of *P. rana* has 17 dorsoventral files, specimens with the dorsoventral file complement may be referred to *P. rana rana*.

The widespread Centerfield (basal Tioughniogan) fauna marks the disappearance of all 18 dorsoventral file *P. rana* and the first incursion of 17 dorsoventral *P. rana* west of the exogeosyncline. *Phacops rana* has 17 dorsoventral files throughout the entire Tioughniogan (fig. 4).

Another dorsoventral file number variant appears in the Taghanic. Again, a variable population occurs in the exogeosyncline of the east. Specimens from the Apulia member of the Tully limestone of central New York show a range of 15 to 17 files. A collection from AMNH locality 3039 (see fig. 15D), for example, has pre-

dominantly 15 or 17. Collections from other localities (USNM 18, 19; AMNH 3040, AMNH 4) in the Tully show the same variation.

Loss of dorsoventral files is evidently pedomorphic in nature, as the larger specimens in the transitional populations in both the Marcellus and Tully of New York tend to reach the more primitive complement of dorsoventral files. Addition of the final dorsoventral file(s) is seemingly retarded into progressively later stages of ontogeny, until they are ultimately lost.

Phacops rana with 15 dorsoventral files from the Taghanic are all referable to *P. rana norwoodensis* Stumm, 1953. This subspecies occurs in most Taghanic formations known (Upper Cedar Valley of Iowa; Milwaukee Dolomite, Wisconsin; Upper Petoskey, western Michigan; Tully limestone, New York). No *P. rana* are known from the Taghanic of eastern Michigan or northern Illinois.

The one specimen of *P. rana* of possible Chemung age available ("*P. nupera*" Hall, AMNH 496911) is poorly preserved, but has 17 dorsoventral files. Apparently, then, the main stock of *P. rana rana* survived for a while in post-Tully times.

Five specimens of *P. rana* from the Cazenovian of Ohio and Michigan have 15 dorsoventral files. Four are from the Plum Brook shale of Ohio (UMMP loc. D) and a single specimen is known from the upper Ferron Point shale (USNM loc. 2). Although these five specimens have but 15 dorsoventral files, in terms of ornamentation and other morphology they are more similar to the contemporaneous *P. rana* with 18 files than they are to *P. rana norwoodensis* (15 files) from the Taghanic.

FACTOR ANALYSIS AND INTERPOPULATIONAL VARIABILITY

The form of Factor Analysis used to analyze intersample relationships of both cephalon and pygidia factors the transformed data matrix into a matrix of factor coefficients, which are in effect the scores of each individual specimen on each reference vector. Each reference vector, in turn, consists of the score, or relative weight, of the contribution of each of the individual variables to the definition of the vector. Samples thus have a particular distribution when factor coefficients are plotted against a reference vector, and the components of the vector reveal the relative

contribution of each variable to the discrimination.

Two different data transformations were used to study the interrelationships of samples; the mathematics of these transformations were explained previously. The effects of these transformations remain to be considered. Normalization by cases converts each specimen (sample) vector to unit length and thus minimizes the effects of ontogeny and size differences in samples resulting from collecting bias. The factor components, however, reflect the unequal magnitude of the variables; the larger variables have larger absolute variances and thus dominate over smaller variables. The net effect is that the contributions of smaller variables to population discrimination are ignored in the analysis.

Normalization by variable gives all variables a variance equal to unity. Sample vectors are then of unequal length and reflect the absolute size of the specimens. The result is to magnify the effects of ontogeny and for factor coefficients to reflect the absolute size of the specimen. Differences in mean sample length vectors (reflecting sampling biases) could therefore lead to incorrect discrimination if there were significant allometry in the ontogeny of *Phacops*. Normalization by cases following normalization by variables removes the problem, although allometry is insignificant in *Phacops*, and populations can be successfully compared no matter what size range and mean sample vector differences exist between samples. Two different analyses, normalizing the data by variable, one with and one without subsequent normalization by cases, were performed. The two differed little; only the former is presented here.

NORMALIZATION BY CASES ONLY

A matrix normalized by cases consisting of 329 specimens and 30 variables yielded two significant factors in rotated solution. Components of the two significant rotated factors are given in table 4. Factor 1 essentially consists of high positive loadings on all gross cephalic measurements and a high negative loading on total lens number. This means that a specimen with a high positive coefficient for factor 1 has relatively fewer lenses per given cephalon size than does a specimen with a lower coefficient. Factor 2 is merely the mirror image of factor 1, i.e., specimens are discriminated on lens number

TABLE 4
FACTOR COMPONENTS, CEPHALIC DATA NORMALIZED
BY CASES
(Variables are defined in Table 1)

Variable	Factor 1	Factor 2
GLIP	0.238	0.109
lpL	0.032	0.012
OCL	0.044	0.026
GWCM	0.343	0.149
CL	0.304	0.157
GWE	0.313	0.113
MIGW	0.177	0.062
lpW	0.169	0.057
CWIP	0.093	0.035
MIIPA	0.106	0.027
MIPA	0.148	0.058
OMIA	0.116	0.047
OMA	0.162	0.063
WOC	0.191	0.154
WVS	0.017	0.013
WPL	0.028	0.033
LPA	0.087	0.060
WPAO	0.078	0.016
WPA	0.047	0.037
WBVS	0.450	0.156
LOP	0.027	-0.012
WOP	0.134	0.075
L	0.116	0.028
HGL	0.107	0.046
HVS	0.055	0.048
HEYE	0.100	0.047
LVS	0.093	0.127
LLVS	0.060	0.081
PEG	0.137	0.043
≠ FAC	-0.383	0.915

per cephalon size, but here a high loading indicates a relatively large number of lenses. In factor 1, the relative importance of each variable seems directly proportional to its absolute magnitude, but some smaller variables are also important in factor 2. Specifically, the length of the visual surface (LVS) is positively related to lens number (≠FAC). The length of the ocular platform from the rear margin of the eye to the posterior border furrow (LOP) is negatively related to lens number. In general, normalization by cases allows discrimination on the basis of over-all eye size, particularly length and total lens number, all at a given over-all cephalic size.

Figure 9 shows the distribution of mean sample factor coefficients for the first rotated

factor plotted against the stratigraphic positions of the samples. Such a diagram is not intended to be read as a simple procession of phylogenetic events, but merely as a means of assessing variation among quasicontemporaneous samples. Sample abbreviations and size are given in table 5. The nine Cazenovian samples plotted show a considerable range in variation. CARD represents the early, variable population, with both 18 and 17 dorsoventral files. All other samples have 18 dorsoventral files except PLUM (15) and STAF (17). Since high loadings on factor 1 indicate relatively few lenses per cephalon size, it is apparent that the main variation within the Cazenovian in total lens number is based on number of lenses per dorsoventral file rather than number of dorsoventral files. Discrimination is therefore based on the *milleri* and *crassituberculata* eye variants (both with 18 dorsoventral files), discussed below.

In terms of general eye morphology, the 17 dorsoventral file population (STAF) is more similar to the *crassituberculata* variant (e.g., SILC, SCRK), and figure 9 shows that *P. rana* samples above the Cazenovian apparently are closer morphologically to *P. rana* with the *crassituberculata* eye variant. Typical *crassituberculata* show very high scores, i.e., have relatively fewer lenses per cephalon size than typical *milleri*-variant populations (e.g., SILM, ARKA).

Variation is considerably compressed and dispersion relatively uniform throughout the Tioughniogan history of *P. rana*. In the upper Tioughniogan there is an increase in lens number per cephalon size which amounts to a convergence on the earlier *milleri* eye variants of the Cazenovian. Clarkson's specimen (1966b, p. 468) of a "*P. rana milleri*" from western New York probably came from a unit such as the Windom member of the Moscow Formation (WINC). Figure 9 shows that the eye morphology of the 17 dorsoventral file specimens from upper Tioughniogan formations are secondarily convergent on the 18 dorsoventral file *milleri* eye variants.

The variation shown by quasicontemporaneous populations within the Tioughniogan seems to be correlated with gross sedimentological features of the various formations. Most Cazenovian formations that produce *milleri*-eye variant specimens in abundance are highly calcareous shales. Throughout the Tioughniogan

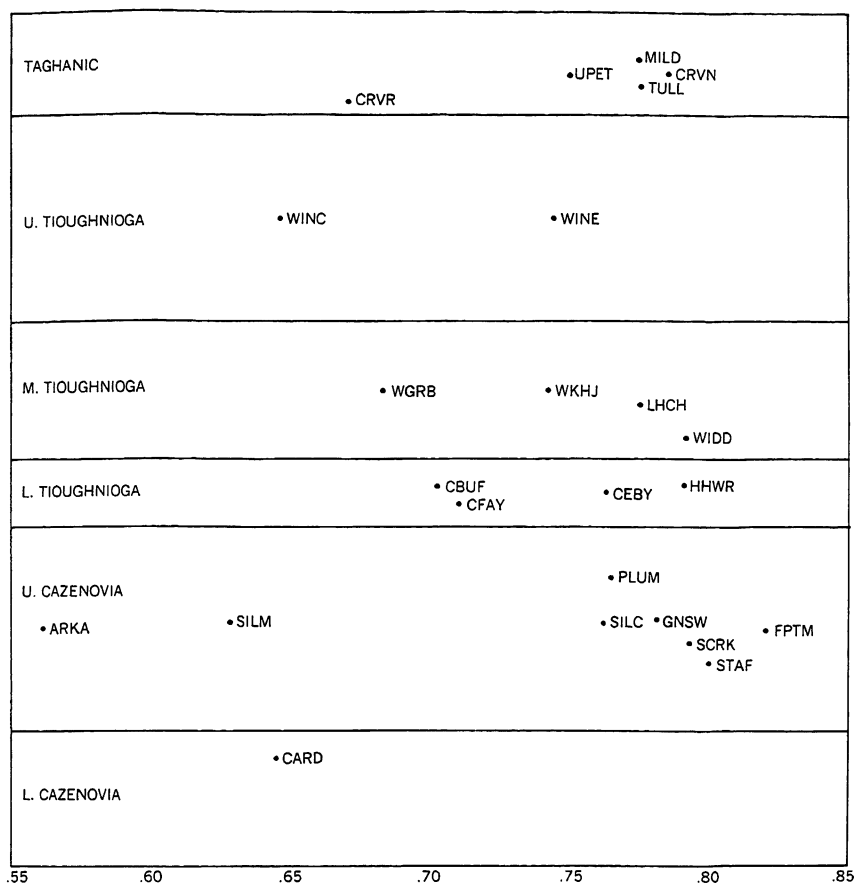


FIG. 9. Factor analysis of *P. rana* cephalon. Data normalized by samples. Mean score for each sample for factor 1 (rotated) plotted against approximate stratigraphic position. Sample abbreviations as in table 5. Factor components are given in table 4.

gan lineage, samples with the highest mean scores on factor 1 occur in more clastic rocks. WINE and LHCH are samples from the Moscow and Ludlowville formations respectively from the Chenango Valley in New York. Both formations are variable shale-siltstone sequences with a low calcareous content. Specimens from purer limestones (CEBY, HHWR) also tend to score relatively high. Samples from fine-grained argillaceous sediments with a high calcareous content (e.g., Tioughniogan shales from western New York—WINC, WGRB) similar to *milleri*-bearing rocks of the Cazenovian, show relatively lower loadings, i.e., a greater proportional number of lenses per cephalon size.

The two major apparent exceptions include CBUF, a population from the Centerfield

limestone in western New York, which scores rather low, and WIDD, representing a sample from the Widder Formation of Ontario (UMMP 4993 and 27066). The Widder is a variable sequence of calcareous shales and limestones; the specimens are very similar to those collected by the author from the underlying Hungry Hollow Formation, which is a Centerfield equivalent. The Hungry Hollow was named by Cooper and Warthin (1941), and includes 6 feet of shale and limestone formerly assigned to the Widder Formation. The UMMP collection was made prior to recognition of the Hungry Hollow, and in view of the identical scores of WIDD and HHWR, there is perhaps some justification in considering the UMMP Widder sample as having come from the Hungry Hollow.

There is an abrupt break between specimens

TABLE 5
FACTOR ANALYSIS PLOTS

Sample	Formation	Locality	N ₁	N ₂	No. Dorsoventral Files	Taxon
ALPI	Alpena limestone	AMNH 3059	10	10	13	Pia
APPM	Hamilton	s. Appalachians	3	3	18	Prm
APPR	Hamilton	s. Appalachians	2	2	17	Prr
ARKA	Arkona shale	UMMP A, B	17	15	18	Prm
BELI	Bell shale	UMMP 31	1	1	13	Pia
CARD	Cardiff	AMNH 3013	5	4	17-18	Prc-Prr
CBUF	Centerfield	AMNH 3047	9	9	17	Prr
CEBY	Centerfield	AMNH 3044	13	13	17	Prr
CFAY	Centerfield	AMNH 3033	6	6	17	Prr
CRVI	Cedar Valley	SUI 4	3	3	13	Pii
CRVM	Cedar Valley	float	1	1	18	Prm
CRVN	Cedar Valley	SUI, various	6	5	15	Prn
CRVR	Cedar Valley	SUI, various	3	3	17	Prr
DSCI	Dock Street	UMMP 53	1	1	13	Pii
FDMI	Four Mile Dam	AMNH 3061	3	3	13	Pii
FPTM	Ferron Point	UMMP 1A	5	5	18	Prm
GNSW1-3	Genshaw	USNM 3	3	3	13	Pia
GNSW4-5	Genshaw	USNM 3	2	2	18	Prm
GPTI	Gravel Point	AMNH 3060	2	2	13	Pia
HHWI	Hungry Hollow	AMNH 3054	1	1	13	Pis
HHWR	Hungry Hollow	AMNH 3054	5	5	17	Prr
LHCH	Ludlowville	AMNH 3031	11	11	17	Prr
MILD	Milwaukee	UMMP G	11	11	15	Prn
NRPT	Norway Point	UMMP III	1	1	13	Pii
PLUM	Plum Brook	UMMP D	4	4	15	Prp
SCRK	Silver Creek	AMNH 6, 6A	13	13	18	Prc
SILC	Silica Shale	UMMP E	28	28	18	Prc
SILM	Silica Shale	UMMP E	35	34	18	Prm
STAF	Stafford	NYSM 2	13	13	17	Prr
THBY	Thunder Bay	UMMP 35	1	1	13	Pii
TULL	Tully	AMNH 3039	16	16	15-16-17	Prr-Prn
UPET	Upper Petoskey	UMMP 7b	2	1	15	Prn
WGRB	Wanakah	AMNH 3049	28	27	17	Prr
WIDD	Widder	UMMP A, B	7	7	17	Prr
WINC	Windom	AMNH 3052	20	18	17	Prr
WINE	Cooperstown	AMNH 3034	15	15	17	Prr
WKHJ	Wanakah	AMNH 3041	23	23	17	Prr
Totals			329	320	—	—

Symbols: N₁, number of specimens per sample, normalizing by cases. N₂, number of specimens per sample, normalizing by variable, then by cases. Pia, *P. iowensis alpenensis*; Pii, *P. iowensis iowensis*; Pis, *P. iowensis southworthi*; Prc, *P. rana crassituberculata*; Prm, *P. rana milleri*; Prn, *P. rana norwoodensis*; Prp, *P. rana paucituberculata*; Prr, *P. rana rana*.

with a relatively large number of lenses per cephalon size in the Upper Tioughniogan, and those with relatively fewer in the Taghanic. There is little variation along factor 1 among the 15 dorsoventral file Taghanic samples. The sudden displacement toward a high loading is partially explained by the fact that most specimens in the Taghanic have but 15 dorsoventral files.

NORMALIZATION BY VARIABLES AND BY CASES

A matrix normalized first by columns (variables), then by rows (cases) consisting of 329 specimens and 28 variables yielded four significant factors in rotated solution. In this analysis, the width of the visual surface and the total number of lenses were omitted. The third and fourth factors, although representing a very

small percentage of the total variance of the matrix, are considered "significant" by virtue of the seemingly important biological information contained in the vector equations and the apparent "sense" made by the relative scores of the various samples. In a previous study (Eldredge, 1968) a similar case was presented in which a single factor, explaining a very small amount of the variance of the matrix, had important consequences in the analysis of convergence between two gastropod species.

The vector equations (factor components) for the analysis are given in table 6. Factor 1 is based largely on the character LOP—i.e., the distance from the rear of the eye to the posterior border furrow measured exsagittally. High scores of samples on this vector indicate a smaller value for LOP in relation to total cephalon size. This factor is not illustrated

TABLE 6
FACTOR COMPONENTS, CEPHALIC DATA NORMALIZED
BY VARIABLES, THEN BY CASES
(Variables are defined in Table 1)

Variable	Factor 2	Factor 3	Factor 4
GLIP	0.117	0.044	-0.178
IPL	0.125	-0.126	0.004
OCL	0.087	0.067	-0.152
GWCM	0.114	0.112	-0.023
CL	0.110	0.032	-0.095
GWE	0.136	0.086	0.111
MIGW	0.124	0.073	0.175
IPW	0.130	0.059	0.154
CWIP	0.174	0.103	0.423
MIIP	0.145	0.086	0.367
MIPA	0.115	0.058	0.240
OMIA	0.115	0.119	0.162
OMA	0.108	0.064	0.149
WOC	0.129	0.051	0.121
WPL	-0.004	0.002	-0.208
LPA	0.101	0.062	-0.105
WPAO	0.171	0.046	-0.128
WPA	0.081	0.105	-0.206
WBVS	0.106	0.055	-0.045
LOP	0.800	-0.041	-0.175
WOP	0.099	0.123	-0.217
L	0.193	-0.036	0.013
HGL	0.095	-0.571	0.339
HVS	0.036	-0.505	-0.140
HEYE	0.072	-0.510	-0.180
LVS	0.009	0.118	-0.161
LLVS	0.007	0.112	-0.201
PEG	0.149	0.017	-0.094

graphically as the mean scores of all samples of *P. rana* fall within a narrow range. The only samples that are effectively discriminated by this factor are: APPM, APPR, LHCH, SCRK, STAF, WINE, HHWR, and WIDD. Of these, the first six consist of exfoliated (internal mold) specimens where LOP is artificially increased owing to the absence of exoskeleton at the rear margin of the eye. WIDD and HHWR have much lower scores (i.e., greater value of LOP) than any other nonexfoliated sample of *P. rana*. The reasons for this apparent anomaly is discussed when the interactions between *P. rana* and *P. iowensis* are considered below.

Factor 2 seems at first glance to be a "mirror image" of factor 1, where a high score indicates a relatively high value for LOP in relation to total cephalon size. Mean scores of samples of *P. rana* are plotted according to approximate stratigraphic position in figure 10. The scores for APPM, APPR, LHCH, SCRK, STAF, and WINE have been omitted for the reason given above. But in factor 2 there does seem to be important interpopulational variability in the relative size of LOP. The range of variation is greatest, again, in the Upper Cazenovian. Tioughniogan and Taghanic samples show, in general, much less variability. Tioughniogan samples are closest to the upper end of the Cazenovian spectrum, whereas four of the five Taghanic samples fall to the lower end. The similarity in the pattern of variation among samples shown by this factor with the pattern seen in factor 1 (normalizing by cases; fig. 9) indicates that the variation in LOP size is, to a degree, correlated positively with lens number per cephalon size. The only discrepancy is in the Taghanic samples where the absolute number of lenses decreases but LOP remains relatively small. This suggests that the loss of the two dorsoventral files in the Taghanic samples probably was compensated by greater thickness of interlensar scleral tissue rather than by reduction in absolute eye size. Finally, the high (and close) scores of HHWR and WIDD represent a real variation best explained with reference to the interactions between *P. rana* and *P. iowensis*.

Factor 3 (fig. 11) shows a pattern of interpopulational variation similar to that exhibited by factor 2, although the amount of variation among quasicontemporaneous samples is apparently more constant at different periods of

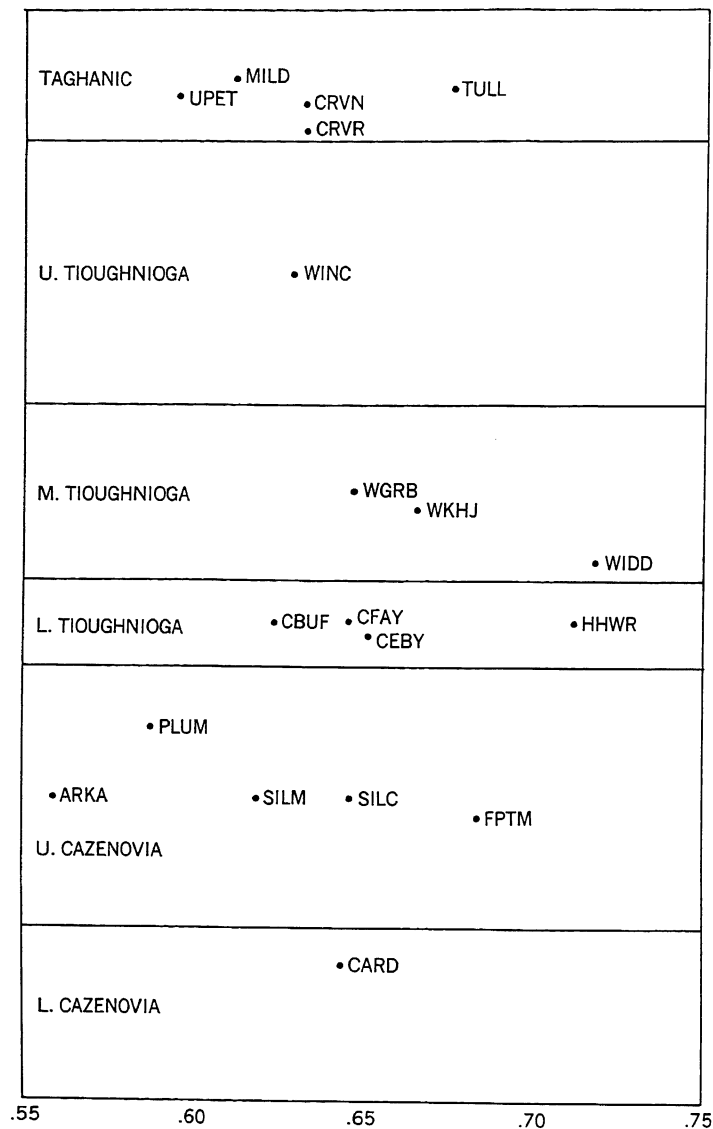


FIG. 10. Factor analysis of *P. rana* cephalia. Data normalized by variables, then by cases. Mean score for each sample for factor 2 (rotated) plotted against approximate stratigraphic position. Sample abbreviations as in table 5. Factor components are given in table 6.

time in factor 3. Here again, the characters underlying this variation are largely related to eye morphology. In factor 3 a high score indicates a small (short) visual surface height and total eye height, as well as a small glabellar height, in relation to total cephalon size. That is to say, all vertical (height) measurements of

the cephalon are varying together; the explanation for the covariance of total eye height and visual surface height with glabellar height is not clear.

The fact that the patterns of interpopulational variation are similar for both factors 2 and 3 again suggests they are related, and that

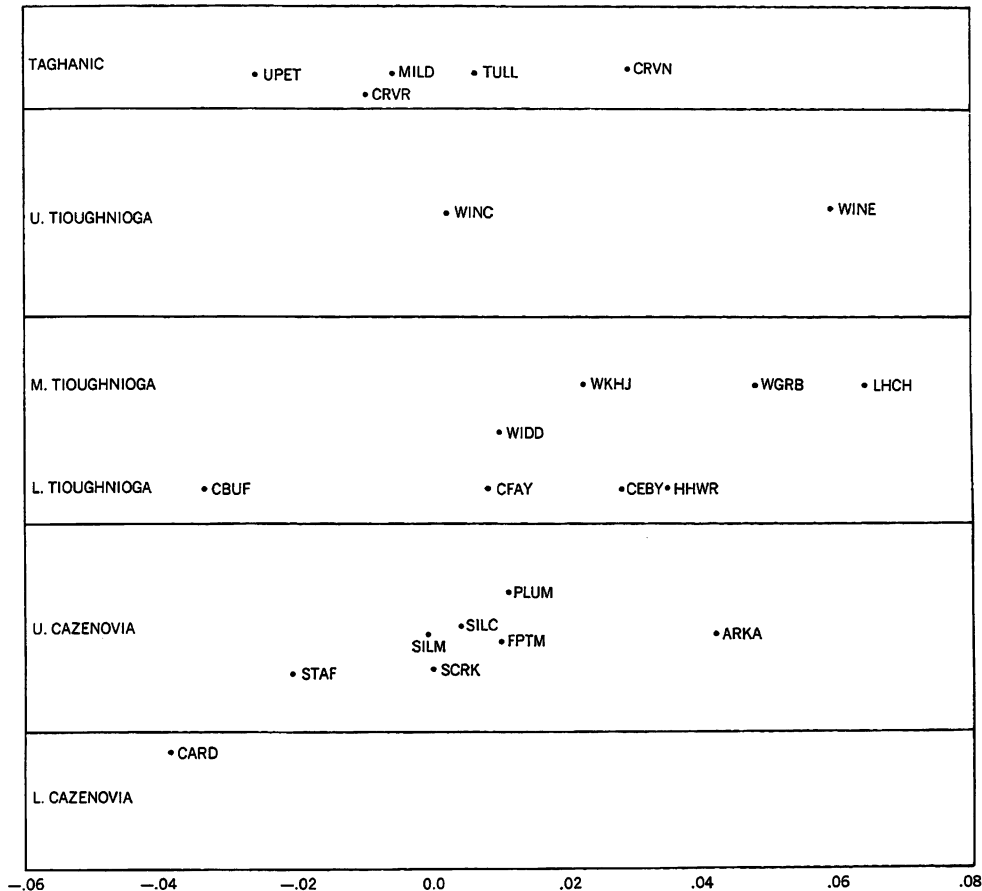


FIG. 11. Factor analysis of *P. rana* cephalon. Data normalized by variables, then by cases. Mean score for each sample for factor 3 (rotated) plotted against approximate stratigraphic position. Sample abbreviations as in table 5. Factor components are given in table 6.

specimens with small LOP values per cephalon size also tend to have a more inflated glabella and, in particular, taller eyes in relation to total cephalon size. In other words, factors 2 and 3 show different aspects of interpopulational variation in total eye size in *P. rana*. Most Cazenovian populations, especially those of the *milleri* eye variant, tend to have a relatively larger number of lenses per dorsoventral file than other samples, and it is not surprising that their eyes are relatively taller than those of most Tioughniogan samples. However, the *milleri* sample from the Arkona shale of Ontario (ARKA) has an anomalously high score in factor 3. Again, the low scores of the 15 dorsoventral file samples in the Taghanic imply that loss of two dorsoventral files was compensated by an increase in thickness of interlensar scleral

tissue, and not by reduction in height of the eye.

The equation for factor 4 (table 6) is perhaps the most interesting of the entire analysis, as it effectively segregates into three distinct groups all length and width measurements and measurements related to the eye. Very simply, a high mean population sample score on factor 4 (fig. 12) indicates a broader, shorter cephalon (in terms of axial measurements) with a smaller eye complex. Here glabellar height varies positively with axial widths. Again, the spectrum of variation seems widest in the Upper Cazenovian. Variability is also extensive among "Centerfield" (basal Tioughniogan) populations, but somewhat less so in the Middle Tioughniogan (but see WKHJ). Here again, the scores of the Tioughniogan samples fall at one end of the spectrum of variation among Cazenovian

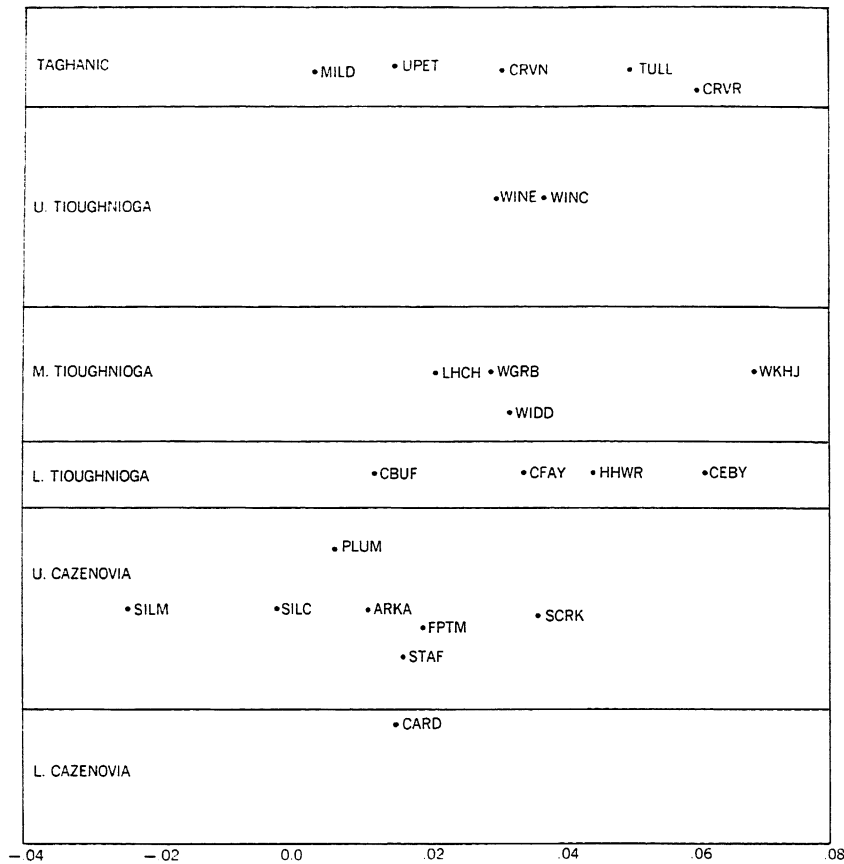


FIG. 12. Factor analysis of *P. rana* cephalata. Data normalized by variables, then by cases. Mean score for each sample for Factor 4 (rotated) plotted against approximate stratigraphic position. Sample abbreviations as in table 5. Factor components are given in table 6.

samples. Cazenovian samples tend to have larger eyes, and narrower, longer cephalata, than Tioughniogan samples; two samples from the Taghanic (MILD, UPET), fall within the range of some of the Upper Cazenovian samples, but the remainder of the Taghanic samples are similar to those of the Tioughniogan.

In summary, factor analysis has added a few linear measurements to the list of important interpopulational variables in *P. rana*. These are: (1) number of lenses per cephalon size, (2) LOP, (3) HVS, HEYE, HGL, and (4) clusters of axial lengths, axial widths, and eye size taken together. It is clear, then, as in the qualitative analysis presented above, that it is the various aspects of eye morphology that show the most significant amount of interpopulational variability in *P. rana*.

SYSTEMATIC PALEONTOLOGY

Four subspecific nomina (*P. rana crassituberculata*, *P. rana milleri*, *P. rana rana*, and *P. rana norwoodensis*) were somewhat casually introduced during the discussion of interpopulational variability in dorsoventral file number. These subtaxa, plus a fifth yet to be introduced, occupy definite subsets of the spectrum of variation in the other characters discussed. These differentiating characters are set forth formally in the following taxonomic diagnoses.

Phacops rana crassituberculata Stumm, 1953

Phacops rana crassituberculata STUMM, 1953, p. 136-137, pls. 9, 10.

Phacops rana crassituberculata: CLARKSON, 1966b, p. 470, pl. 73

Figure 13A-D

EMENDED DIAGNOSIS: Eye with 18 dorso-ventral files in normal adults. Maximum number of lenses per file six, rarely seven. Interlensar sclera well developed, hexagonal; lenses generally flush with sclera except on the ventral portion of the visual surface in immature specimens.

Tubercles large and bluntly rounded on composite glabellar lobe, decreasing in size and becoming transversely elongate posterior to anterior glabellar slope. Transverse elongation of tubercles becoming increasingly extreme

anteriorly, tubercles becoming wavy ridges at anterior cephalic margin. Tubercles of occipital lobe similarly transversely elongate. Tuberculation only moderately developed over genae. Tubercles usually small, occasionally sharply pointed, on palpebrum.

Trace of facial suture over ocular platform quite shallow. Genal angles bluntly pointed.

Pleura of pygidium rather flat; pleural furrows rather shallow. Anterior interpleural furrow occasionally developed.

HOLOTYPE: UMMP 25537.

STRATIGRAPHIC DISTRIBUTION: Cazenovian. The distribution of this subspecies is given in table 8.

Phacops rana milleri Stewart, 1927

Phacops rana var. *milleri* STEWART, 1927, p. 58, pl. 5.

Phacops rana var. *milleri*: DELO, 1940, p. 23-24, pl. 1.

Phacops rana milleri: STUMM, 1953, p. 137-138, pls. 9, 10.

Phacops rana arkonensis STUMM, 1953, p. 138-139, pl. 10. non *Phacops rana milleri* CLARKSON, 1966b, p. 468-470, pl. 73.

Figure 14A-D

EMENDED DIAGNOSIS: Eye with 18 dorso-ventral files in normal adults. Maximum number of lenses per file nine. Horizontal interlensar sclera variably developed, usually in upper one-third of each dorsoventral file only. Lenses generally protruding from scleral surface in all but dorsalmost rows.

Remainder of cephalic features as in *P. rana crassituberculata*, except tuberculation more weakly developed, and more rounded on palpebrum.

Thorax and pygidium as in *P. rana crassituberculata* except tubercles less strongly developed, approaching obsolescence.

SYNTYPE: Department of Geology, Ohio State University 16266 (not examined).

STRATIGRAPHIC DISTRIBUTION: Cazenovian. The distribution of this subspecies is given in table 8.

Phacops rana norwoodensis Stumm, 1953

Phacops rana norwoodensis STUMM, 1953, p. 140, pl. 12.

Figure 15A-D

EMENDED DIAGNOSIS: Eye with 15, rarely 16 or 17, dorsoventral files. Trace of facial suture across ocular platform moderately deeply incised.

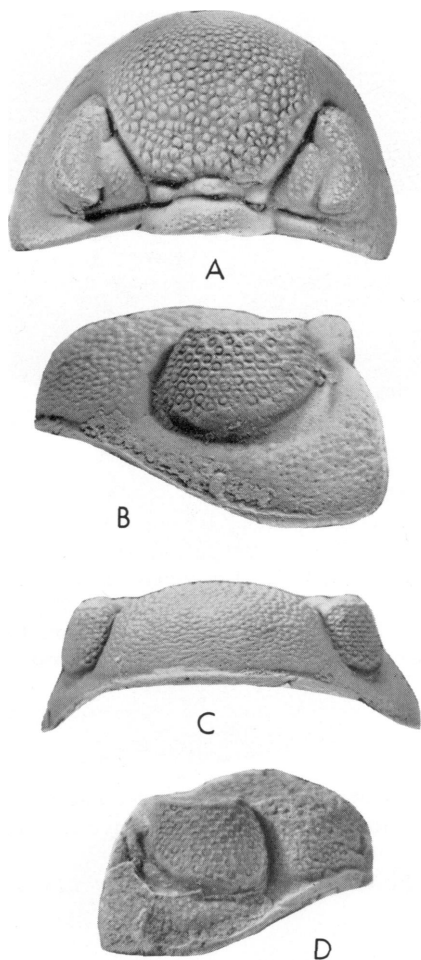


FIG. 13. *Phacops rana crassituberculata* Stumm, 1953. A-C. Silica shale, AMNH locality 3063, AMNH 28898. A. Dorsal view of cephalon, $\times 2$. B. Left lateral view of cephalon, $\times 3$. C. Frontal view of cephalon, $\times 2$. D. Right lateral view of cephalon, Solsville Member, AMNH locality 3013, AMNH 29119, $\times 3$.

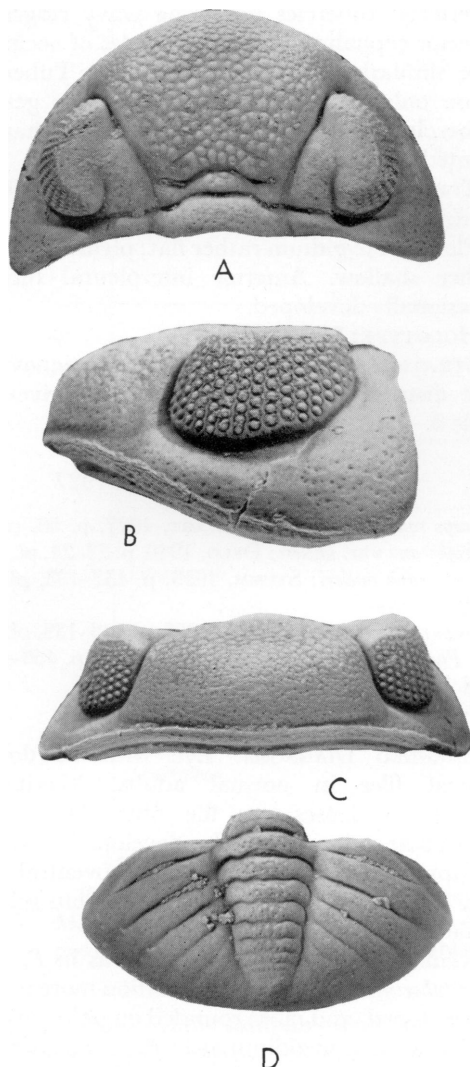


FIG. 14. *Phacops rana milleri* Stewart, 1927. Silica shale, AMNH locality 3063. A–C. AMNH 28896. A. Dorsal view of cephalon, $\times 2$. B. Left lateral view of cephalon, $\times 3$. C. Frontal view of cephalon, $\times 2$. D. Dorsal view of pygidium, AMNH 28897, $\times 3$.

Elongation of cephalic tubercles usually restricted to anterior glabellar margin, genal margins, and posterior row of tubercles on occipital lobe. Tubercles variably densely or sparsely distributed over composite glabellar lobe. Genal angles as in *P. rana rana*.

Pleural furrows deeply incised and pleura highly arched for species.

HOLOTYPE: UMMP 25524.

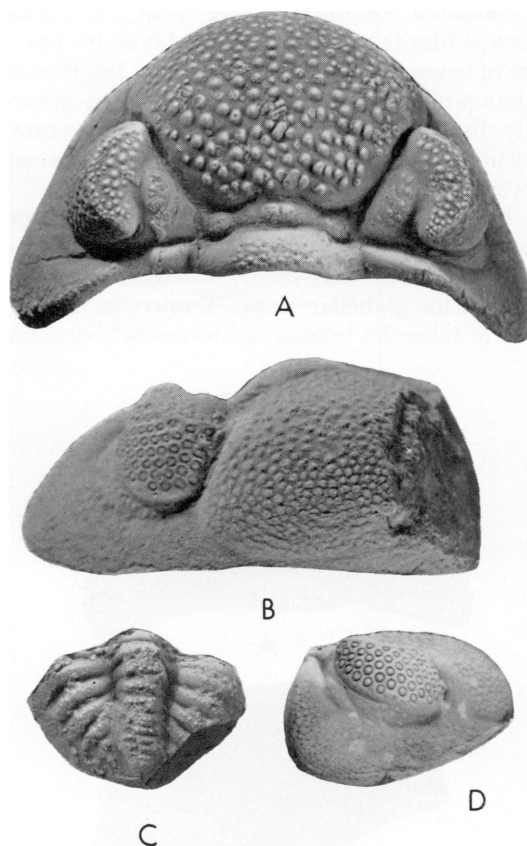


FIG. 15. *Phacops rana norwoodensis* Stumm, 1953. A. Dorsal view of cephalon, paratype, Milwaukee dolomite, UMMP locality G, UMMP 14727, $\times 3$. B. Oblique lateral view of cephalon, holotype, Upper Petoskey Formation, UMMP locality 7b, UMMP 25524, $\times 3$. C. Dorsal view of pygidium, Brandon Substage, Cedar Valley Formation, Belanski collection, SUI locality 183–5, SUI 6427, $\times 2$. D. Right lateral view of cephalon, Tully Formation, AMNH locality 3039, AMNH 28899, $\times 3$.

STRATIGRAPHIC DISTRIBUTION: Taghanic. The distribution of this subspecies is given in table 8.

***Phacops rana paucituberculata*,**
new subspecies
Figure 16A–C

DIAGNOSIS: Eye with 15 dorsoventral files in normal adults. Tubercles extremely sparse over composite glabellar lobe, except in single known specimen from outside type area. Remainder of features as in *P. rana crassituberculata*.

HYPODIGN: Four specimens from the Plum

Brook shale of Ohio, (UMMP loc. D). UMMP 25538, 28849, 28850, and 57135 (holotype).

STRATIGRAPHIC DISTRIBUTION: Cazenovian. The only other specimen referred to this subspecies occurs in the Upper Ferron Point Formation.

Phacops rana rana (Green, 1832)

Figure 4A-D

See Diagnosis of species for synonymy.

DIAGNOSIS: Eye with 17 dorsoventral files in normal adult. Trace of facial suture across ocular platform moderately incised.

Tuberculation generally densely distributed over glabella. Transverse elongation of tubercles

developed partially up front slope of glabella, becoming progressively more elongate approaching anterior cephalic margin. Tuberculation of genae and palpebral areas variably developed.

Genal angles bluntly rounded.

Axial rings of thorax and pygidium covered with tubercles moderately elongate transversely.

Interpleural furrows obsolescent on pygidium. Pleural furrows moderately incised; pleura gently rounded. Tuberculation obsolescent on pygidial margins.

HOLOTYPE: NYSM 13887/1.

STRATIGRAPHIC DISTRIBUTION: Cazenovian, Troughniogan, Taghanic, ?Finger Lakes. The distribution of this subspecies is given in table 8.

A THEORY OF RELATIONSHIPS AMONG SUBSPECIES OF *PHACOPS RANA*

Two general problems must be discussed before a general theory of relationships among these five taxa can be elaborated. The first of these involves the new subspecies *P. rana paucituberculata*. Although resembling *P. rana norwoodensis* in having but 15 dorsoventral files, the five specimens known of *P. r. paucituberculata* are identical in all other important interpopulational variation characteristics to *P. rana crassituberculata* and *P. rana milleri*. As mentioned previously, the closest relative to *P. rana* known is the Eifelian European species *P. schlotheimi*, *sensu lato*, recently revised by Burton (MS.b). Burton has shown that the *P. schlotheimi* in the Trilobitenfelder at Gees, Germany, includes a 15 dorsoventral file variant known as *P. schlotheimi latreillii*. In view of the close similarity between *P. r. paucituberculata* and the *P. r. milleri-crassituberculata* complex, and the existence of an apparently equivalent variation in the closest known relative of the *P. rana* group, it is here concluded that the five known Cazenovian specimens of *P. rana* with 15 dorsoventral files are not closely related to the 15 dorsoventral file subspecies *P. r. norwoodensis*, but in fact represent a rare subspecies of *P. rana* whose affinities lie with the 18 dorsoventral file *milleri-crassituberculata* complex.

The second problem to be faced involves the relationship between *P. rana crassituberculata* and *P. rana milleri*. These two taxa are fundamentally alike in terms of the criteria used to distinguish the other subspecies, but differ from each other in other aspects of eye morphology. *Phacops rana*

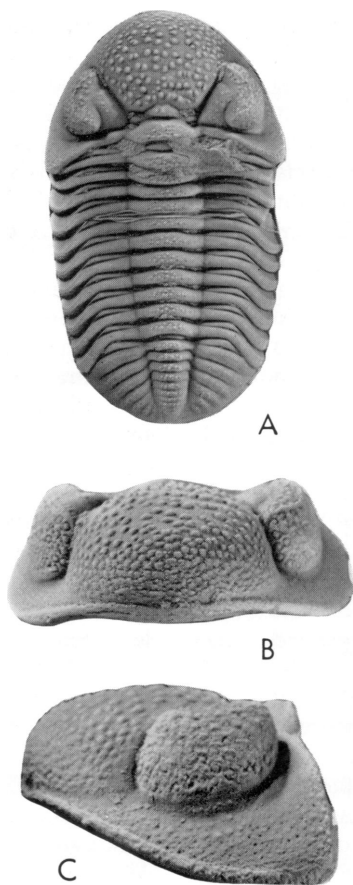


FIG. 16. *Phacops rana paucituberculata*, new subspecies. Plum Brook Shale, UMMP locality D; holotype, UMMP 57135. A. Dorsal view, $\times 2$. B. Frontal view of cephalon, $\times 3$. C. Left lateral view of cephalon, $\times 4$.

milleri and *P. rana crassituberculata* differ primarily in relative number of lenses per dorsoventral file. Both have 18 dorsoventral files. There are up to eight or nine lenses per dorsoventral file in *milleri*, and crowding of so many lenses onto the visual surface left little room for interlensar scleral tissue. Generally, the lenses within a file actually touch each other three-quarters of the way up the height of the visual surface, and the lenses bulge out beyond the scleral surface.

Thus, the appearance of the lower three-quarters of the visual surface in *milleri* is similar to the lower one-third or so of the visual surface of other subspecies. Apparently the rate of lens addition is very high and persists later into ontogeny than is usual in other subtaxa of *P. rana*. The *crassituberculata* variant generally has a maximum of six lenses per dorsoventral file and is distinguished from *P. rana rana* in terms of eye morphology solely by possession of 18 dorsoventral files. Factor analysis (fig. 9) shows that in terms of lens number per eye, typical populations of *crassituberculata* (e.g., SILC, SCRK) are close to later populations of *P. rana rana*, whereas typical populations of the *milleri* variant (ARKA, SILM) seem less closely related to *P. rana rana*. Furthermore, this type of eye variation is not encountered above the Cazenovian, or even within Cazenovian populations with 17 dorsoventral files, although upper Tioughniogan *P. rana rana* secondarily converges on the *milleri* condition.

At least three plausible explanations may be considered for the existence of the two eye variants. Clarkson (1966b, p. 467) has tentatively suggested that the eye variants may reflect sexual dimorphism. Alternatively, the variation

may be a polymorphism reflecting a broad ontogenetic norm of reaction reflecting local ecological conditions. A third possibility is that the variants represent true geographic races.

The distribution of the two variants is given in table 7. Both Stewart's types of *milleri* and Stumm's types of *crassituberculata* come from the Silica shale of Ohio and represent extremes. Specimens from other stratigraphic units are occasionally more difficult to classify. Although specimens from the Silver Creek limestone of Indiana are definitely *crassituberculata*, collections from the St. Laurent limestone of Illinois and units elsewhere are of a more intermediate character. Generally, however, any single formation will produce one or the other, but not both variants. The important exception is the Silica shale. The biostratigraphy of *Phacops* within the Silica shale reveals that most of the units recognized by Ehlers, Stumm, and Kesling (1951) contain only one of the eye variants, or at least an overwhelming predominance of one variant over the other. For example, unit 9 is a relatively thin calcareous shale unit containing abundant specimens of the *milleri* variant. The *crassituberculata* variant is extremely rare in unit 9. Conversely, *crassituberculata* far outnumber *milleri* in the underlying unit 8, which is a limestone (M. Widener, personal commun., 1968). Although specimens have been found with cephalon of both of the two variants associated on the same bedding plane, in general *crassituberculata* is to be found in the limestones and the denser, more calcareous shales of the Silica Formation, whereas *milleri* occurs in the more argillaceous units. The distribution of the variants given in table 7 indicates that this sediment preference holds generally true throughout the distribution of the two eye variants. It will be recalled that, for the species as a whole, factor analysis (fig. 9) indicated that samples from highly calcareous shales in general tended to have a greater number of lenses per cephalon size than those from more argillaceous or purely limestone units.

The eyes of all small post-larval instars of *P. rana* collected from the Silica shale appear to be of the *milleri* variety. Absence of any small specimens clearly referable to the *crassituberculata* variant indicates that the early ontogenetic development of the two variants is identical. Rare but definite occurrences of specimens referable to both variants on the same bedding

TABLE 7
DISTRIBUTIONS OF *Phacops rana crassituberculata* AND
Phacops rana milleri

<i>P. r. crassituberculata</i>	<i>P. r. milleri</i>
Silica shale	Silica shale
Dundee limestone	Bell shale
Saint Laurent limestone	Upper Ferron Point shale
Lower Arkona shale	Upper Arkona shale
Silver Creek limestone	Genshaw Formation
Lower Ferron Point shale	Lower Romney
Deputy limestone	Lower Rockport Quarry limestone
Cardiff shale and siltstone	—

plane also indicates that the hypotheses of ecological or geographic races is incorrect. Sexual dimorphism must also be rejected in view of the stratigraphic and geographic distributions of the two variants. The precise nature of the relationship between *milleri* and *crassituberculata* seems an insoluble problem with the given data as the correct explanation appears to lie in the realm of population genetics. Perhaps the ontogeny of the eye was flexible and capable of reaction to the peculiar environmental conditions obtaining at a given place at a given time. Alternatively, a more strictly genetically based adaptation to local environments may underlie the distributions of the two variants. No model seems to be available that satisfactorily accounts for all the morphological and distributional data of these closely related variants.

Nevertheless, population samples can generally be referred to one or the other eye variant. The variants were also generally distinguished in factor analysis (see figs. 9–12). In view of the

geographic distribution and the relative ease in recognition of the two variants, it is perhaps best to continue to recognize the variants as distinct subspecies: *P. rana milleri* and *P. rana crassituberculata*. It must be remembered, however, that the relationship between those two subspecies is of a different nature than the relationships between both of them and the other three subspecies recognized here.

In terms of dorsoventral file number only, the five subtaxa of *P. rana* can be arranged in a gradational manner as in figure 17A. Figure 17B shows a similar gradational arrangement based on ornamental and other characters discussed above. These *character gradients* are highly intercorrelated; there is no "mosaic" pattern of different combinations of character states among different samples. The two diagrams differ only in that *P. rana paucituberculata* is included with the *crassituberculata-milleri* group in figure 17B. It has already been concluded that this second arrangement is probably a more accurate reflection of the true affinities of *P. r.*

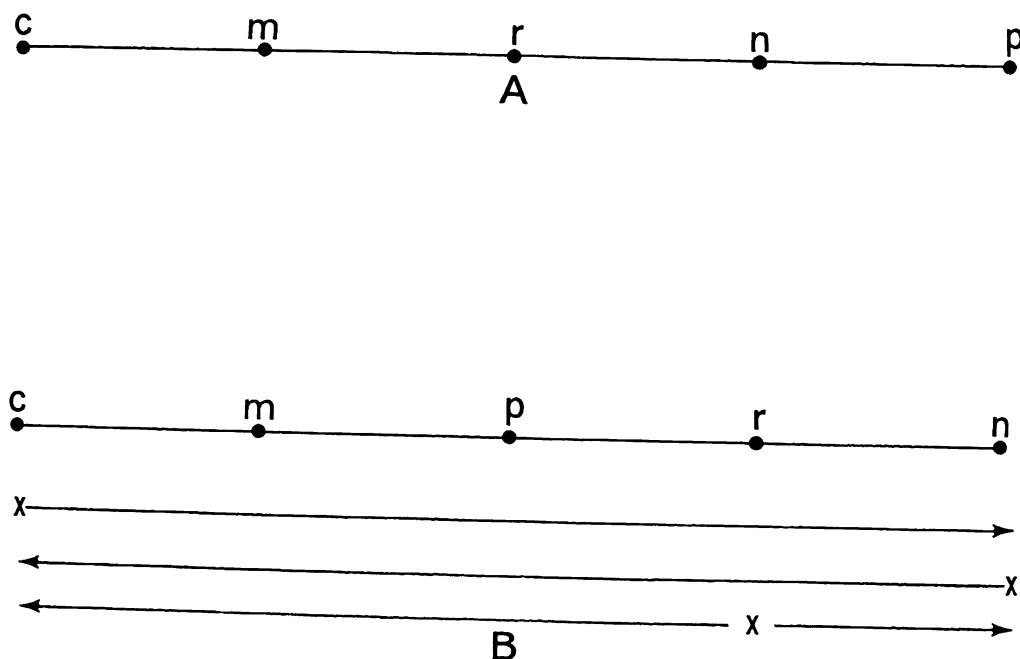


FIG. 17. Diagram of character gradients. A. Taxa arranged strictly according to number of dorsoventral files. B. Taxa arranged according to all other qualitative characters as discussed in text. Along each axis the primitive condition is indicated by an X and the direction of the arrow indicates the derived condition(s). c – *P. rana crassituberculata*; m – *P. rana milleri*; n – *P. rana norwoodensis*; p – *P. rana paucituberculata*; r – *P. rana rana*.

paucituberculata. Consequently, the 15 dorsoventral file condition is thought to have evolved twice within the *P. rana* complex as a whole. In view of the parallel, intercorrelated nature of all these character states (including ornament, genal angle and ocular platform morphology of the cephalon, and morphology of the pygidium), there are but three possibilities as far as primitive versus derived conditions of these characters are concerned. These possibilities are indicated by arrows under figure 17B, where the primitive condition is indicated by an X, and the derived condition by the arrow point. Characters shown by factor analysis to be important interpopulational discriminants in general do not show the same type of gradation between subtaxa depicted in figure 17B and are not discussed further herein.

Although arrangements 1 or 2 may seem more economical hypotheses than arrangement 3, there is really little basis for preference for any one of the three possible primitive-derived relationships outlined in figure 17B. The only character that affords some definite data by which primitive and derived conditions can be assessed is dorsoventral file number. Here ontogeny and interpopulational variation do indeed suggest a definite pattern of primitive and derived conditions.

Ontogeny of the eye in both *P. r. milleri* and *P. r. crassituberculata* indicate that the first dorsoventral file is the last of the 18 files to appear in ontogeny. The Solsville Formation near Morrisville, New York (AMNH loc. 3013; see Appendix 2) provides the only known sample in which there is intrapopulational variability between the 18 and 17 dorsoventral file conditions. As generally only the larger cephalata in this population sample possess an eighteenth file (dorsoventral file no. 1), and this file is incompletely developed in some specimens, the data suggest that the 17 dorsoventral file condition was derived pedomorphically from the 18 dorsoventral file condition. Furthermore, the main variants of the *P. schlotheimi* complex, here considered the closest known relative of *P. rana*, have 18 dorsoventral files. The best hypothesis, then, seems to be that the 18 file condition is primitive for *P. rana*.

No ontogenetic or interpopulational variability data exist for *P. r. paucituberculata*, but in view of its close relationship by all other criteria to the *milleri-crassituberculata* complex, its 15

dorsoventral files must be assumed to have been derived directly and independently from the 18 file condition. The variation in dorsoventral file number in various samples of *P. rana* from the Tully limestone of New York has been discussed above. Amount of variation differs from place to place. In the more argillaceous West Brook Member in the more eastern part of New York, all specimens retain 17 dorsoventral files. In the Apulia Member (a fine-grained limestone) farther west, populations showing differing amounts of variation in dorsoventral file number have been collected. In a collection from South Lansing, New York (AMNH loc. 3039), most cephalata have but 15 dorsoventral files, but a few of the larger cephalata possess 16 or 17. Although the data are not quite so definitive as in the case of the 18–17 dorsoventral file relationship, there are grounds for preferring the hypothesis that 17 dorsoventral files is primitive with respect to the 15 file condition of Taghanic *P. rana*. A theory of relationships based on dorsoventral file number is presented in figure 18.

If this view of the relationships of the subtaxa of *P. rana* is substantially correct, we have some basis for preferring arrow no. 1 in figure 17B as most likely representing primitive-derived conditions in all the other characters of the character gradient. However, there is no real biological proof that this is so. When this gradient, and the apparent sequence of primitive-derived dorsoventral file number conditions are reviewed below in conjunction with *P. iowensis*, stronger reasons emerge for viewing arrow no. 1 in figure 17B as the true axis of primitive-derived conditions.

When this view of the relationships among the five subtaxa of *P. rana* is compared to the known stratigraphic record, and particularly first appearance, of these subspecies, a rough coincidence between stratigraphic position and adjudged primitive-derived conditions emerges. Not surprisingly, there is a basic agreement between the order of inferred phylogenetic events and the stratigraphic occurrence of the various subspecies. But to what extent may it be said that the stratigraphic record provides an ancestral-descendant sequence for these taxa? The theory of relationships is, in a sense, testable, but a rigid ordering of an ancestral-descendant sequence, with or without concurrent stratigraphic data, is not. Consequently,

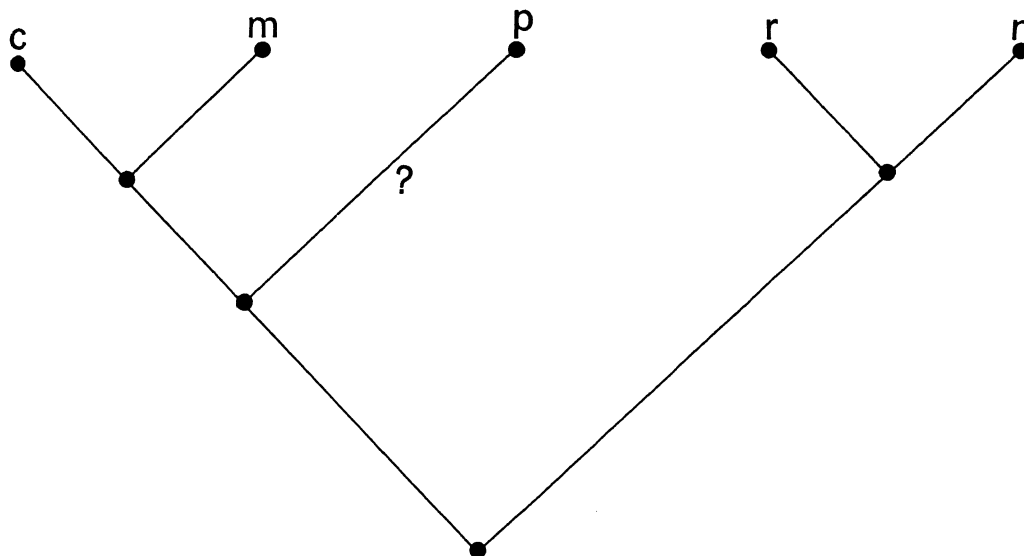


FIG. 18. Theory of relationships among the five subspecies of *Phacops rana*. Abbreviations as in figure 17.

no claim that *P. rana crassituberculata* is ancestral to *P. rana rana*, or that *P. rana rana* is ancestral to *P. rana norwoodensis*, is admissible in any strict sense. It must be recognized that the samples on which the analysis of the interrelationships was based should not be construed as actual ancestors to any such (stratigraphically) subsequent samples, but rather constitute samples of taxa related in an unknown manner by common ancestry to the subsequent samples.

With this proviso in mind, once a theory of interrelationships of the taxa concerned has been worked out on strictly biological criteria, and if the stratigraphic record is at least in some accord with the inferred sequence of phylogenetic events, the paleontologist is free to speculate on the nature of these phylogenetic events on the basis of his samples. His statements, however, are largely untestable. But the concept of the fossil record as a laboratory for analyzing evolutionary experiments is very appealing, affording as it does the only opportunity available to the evolutionist to study phylogenetic patterns over a formidable period of time. It would be fruitless, in my view, to abandon this potential for comparing apparent patterns with known processes simply because the concept that the fossil record preserves a biostratigraphic pattern of phylogeny which may be read directly is biologically naive. With

appropriate attention paid to all assumptions, a best fit "model" for a reconstructed pattern of phylogenetic events may be elaborated, with the potential for rejection should new, contradictory evidence appear.

Various aspects of the evolutionary process may be investigated under these conditions. Among these, "trends," modes of speciation, and interspecific interactions are discussed in conjunction with *P. rana* and *P. iowensis*. The term "trend" is used herein perhaps in a slightly different sense than is usual. Two difficulties, in particular, lie in the usage of this term. The preponderant model used in paleontology for the origin of new infrataxa (species, etc.) has involved gradual, linear change instead of the allopatric model accepted by most neontologists (Eldredge, 1971). As a consequence the tendency is to look to a stratigraphic sequence to reveal gradual, progressive evolutionary changes —i.e., trends. Thus, demonstration of biostratigraphic trends may form the basis for the analysis of the interrelationships among the taxa involved, which is tantamount to assuming what is to be proved, and which may easily result in an incorrect interpretation of phylogeny. This constitutes one of the problems that may be encountered when establishing ancestral-descendant relationships on the basis of biostratigraphical data.

Lack of adequate attention to allopatric phenomena raises a second, more substantive problem regarding trends. The problem is one of reconciling the process of adaptation to local edaphic conditions by a peripheral isolate—an important point in the general theory of allopatric processes—with long term, net change in morphological structures which we refer to as “trends.” As Wright (1967) has remarked, in the context of the evolution of higher taxa, speciation is a stochastic process. It seems that adaptation to local edaphic conditions by peripheral isolates should also be stochastic in the context of long-term trends. In this light, it is possible that the pervasiveness and importance of anagenesis (Huxley, 1958), with its attendant connotation of “general improvement” may have been overemphasized in recent discussions (e.g., see Gould, 1970).

In the present study, then, the term trend is applied to a demonstrated character gradient (between interrelated taxa), which has been shown to appear in the stratigraphic record in the inferred order of its evolution. The samples used to document the trend are related in terms of recency of common ancestry, and no ancestral-descendant relationships between samples are claimed. The discussion is strictly within the context of the history of the entire group being considered (in this case the entire biospecies *P. rana*) and involves taxa definitely known not to have been ancestral to subsequent samples as well as those which may or may not have been in fact ancestral to subsequent samples. It is simply a “statistical” characterization of the status of the entire species *Phacops rana* at successive stratigraphic intervals. Amount of variability among quasicontemporaneous samples, as well as any apparent linearity in direction of change can be related to adaptation to ecological parameters (including other species) just as easily as if the assumption were made that the successive samples were actual documents of progressive, phyletic change strung out in an ancestral-descendant sequence.

TRENDS (BIOSTRATIGRAPHIC CHARACTER GRADIENTS) IN *PHACOPS RANA*

All characters, including linear measurements, shown to be important interpopulational variables, have particular “values” in each of the subspecies. In view of the different biostratig-

raphic ranges of these subtaxa, all of these important variables turn out to possess characteristics of trends. A simple list of these trends, then, is a trivial reiteration of these characters discussed extensively above. However, differences in rate and direction among these character gradients are instructive, as they demonstrate (once again) that, to a degree, different characters may change in different ways (directions, rates) all the while being an important part of a highly “integrated” phenotype. It is well to remember, too, that the great majority of anatomical features in *P. rana* remained essentially stable throughout eight to 10 million years.

Most of these “biostratigraphic character gradients” involve aspects of eye morphology; six major trends involving ornamental and other features are thought to be progressive, i.e., gradual, involving a linear shift at a more or less constant rate from the initial character state in all Cazenovian populations through to the final character state exhibited by populations in the Taghanic. It is essential to emphasize that “gradual” and “progressive” imply changes in “mean” character state; no claim is made that these changes can be documented stratigraphically, e.g., within successive samples of *P. rana rana* within the Tioughniogan. The significance of most of these trends lies in the gradual approximation of *P. iowensis* characteristics by the entire *P. rana* complex through time. These six trends may be summarized briefly as: (a) rounding of the genal angle; (b) deeper incision of the facial suture furrow on the ocular platform, and shift of the librigenal moiety of the ocular platform to a more nearly vertical orientation, so that it becomes confluent with the area under the visual surface; (c) decrease in the amount of flattening and the degree of transverse elongation of ornamental tubercles on the anterior region of the composite glabellar lobe, occipital lobe, and genal margins; (d) increase in strength of tuberculation on the thorax and pygidium; (e) deeper incision of pleural furrows on the pygidium; and (f) eventual loss of interpleural furrows on the pygidium.

Changes in mean character state values can perhaps be documented more closely in the trends involving eye morphology, particularly those seen in factor analysis. Within the context of the preceding discussion on the nature and

significance of trends, the four graphs (figs. 9–12) showing mean population sample scores for a particular factor plotted against approximate stratigraphic position reveal interesting information on modes of morphological change within the *P. rana* group. Thus one may speak of a trend within Tioughniogan *P. rana rana* for increase in total number of lenses per cephalon size (fig. 9). Starting from a mean character state in the general range of the Cazenovian *crassituberculata* eye variant (e.g., SILC), this increase in total lens number through time progressed until Upper Tioughniogan samples (WINC, WINE) fall into the general range of *P. rana milleri*. Reduction in dorsoventral file number from 18 to 17, then, is unrelated to this trend. The abrupt shift in this trend as seen in the Taghanic samples of *P. rana norwoodensis* is due simply to deletion of two additional dorsoventral files.

In factors 2 and 3 (figs. 10, 11) of the second factor analysis, aspects of eye size (height and posterior extent of the ocular platform) result in similar dog-legged plots. Here, the eye in most samples of *P. rana* is reduced in size from the Upper Cazenovian into the Middle Tioughniogan; the trend is then reversed. Again, reduction in number of dorsoventral files is unrelated to trends seen in eye size, since earliest *P. rana* samples with 17 dorsoventral files fall within a portion of the general Cazenovian variation, and reduction from 17 to 15 files necessitates no change in eye size whatsoever. Increase in eye size, rather, seems to be related to increasing the total number of lenses of the eye within the Upper Tioughniogan samples of *P. rana* — a phenomenon solely of increased number of lenses per dorsoventral file.

Factor 4 (fig. 12), involving axial length and width proportions, and over-all size of the ocular complex, shows no pattern of gradual change; Tioughniogan *rana* are all rather similar (though variable), and score closest to a portion of the variation seen in the Cazenovian. Some similarity to the other trends (factors 2 and 3; figs. 10, 11) does appear with the anomalously low scores of MILD and UPET in the Taghanic.

Finally, the grandest trend of all involved reduction from 18 to 15 dorsoventral files. It will be argued immediately below that, far from being gradual, the reductions took place in isolated, peripheral populations in steps, each

event taking a relatively short period of time. Throughout the greater period of the history of *P. rana*, dorsoventral file number was rigidly stable. But, if the theory of relationships among the various subtaxa as presented above is largely correct, it is nevertheless true that all phylogenetic changes in dorsoventral file number involved reduction and never addition of files. A similar over-all trend in dorsoventral file reduction is probably true of the *P. logani*-*P. iowensis* lineage in the Lower through Middle Devonian of North America. Reduction and ultimate loss of eyes in other phacopid lineages, especially in the Upper Devonian of Europe (Richter and Richter, 1955) are of course well known, but it remains to be seen whether these trends were accomplished in the same manner as presented here for *P. rana*. I will not pursue here the adaptive significance of such loss (but see Clarkson, 1967); in view of the convergence in many characters of *P. rana* on *P. iowensis*, however, phylogenetic reduction in dorsoventral file number within the *P. rana* group may reflect convergence toward the 13 dorsoventral file condition of *P. iowensis*, although the functional anatomical reasons for this remain obscure.

MODE OF ORIGIN OF THE SUBSPECIES

Elsewhere (Eldredge, 1971) I have discussed the probable mode of origin of the subspecies of *P. rana* in terms of the allopatric model. It should be noted that the pattern presented in that paper represents merely a hypothesis based on the assumption that the theory of relationships given in detail above is substantially correct. Again, the statement "*P. rana rana* is the ancestor of *P. rana norwoodensis*" should be rewritten: "The common ancestor of *P. rana rana* and *P. rana norwoodensis* possessed (among other important characteristics) 17 dorsoventral files." The further hypothesis that this "common ancestor," if somehow known, would be classified as *P. rana rana* is essentially untestable. However, for reasons set forth in Eldredge (1971), this hypothesis is to be preferred over others, and if correct, leads to interesting insights into modes of speciation among Paleozoic invertebrates in the epicontinental seas. For a further discussion, see Eldredge (1971). The hypothesis of phylogenetic descent in *P. rana* is shown in figure 19.

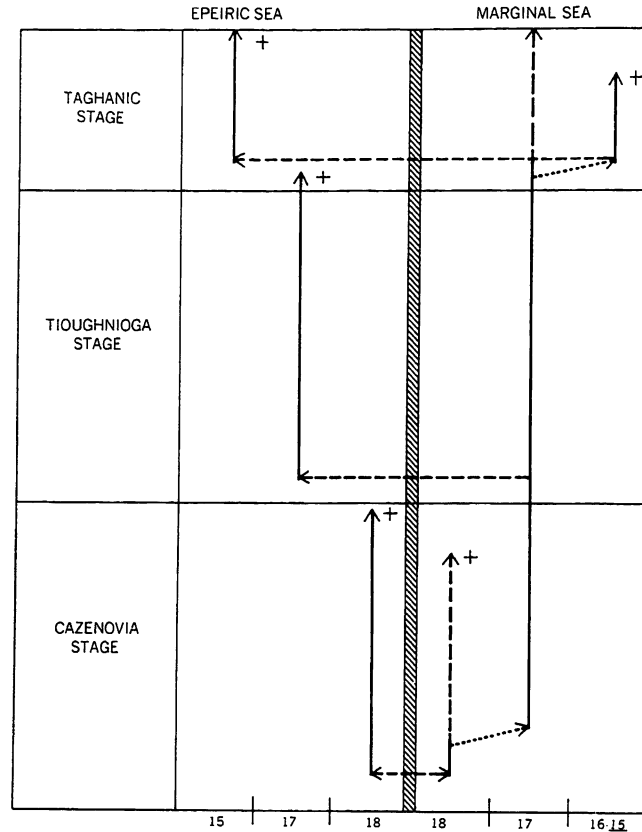


FIG. 19. Hypothesized phylogeny of the *P. rana* stock. Numbers at the base of the diagram refer to the population number of dorsoventral files. Dotted lines: origin of new (reduced) number of dorsoventral files in a peripheral isolate; horizontal dashed lines: migration; vertical solid lines: presence of taxon in indicated area; dashed vertical lines: persistence of ancestral stock in a portion of the marginal sea ("exogeosyncline") other than that in which the derived taxon occurs. Crosses denote final disappearance. The derivation of the 15 dorsoventral file subspecies *P. rana paucituberculata* is omitted from the diagram.

BIOSTRATIGRAPHIC SIGNIFICANCE OF *PHACOPS RANA*

The stratigraphic and geographic distributions of the five recognized subspecies of *Phacops rana* are summarized in table 8. So far as is known, *P. rana milleri* and *P. rana crassituberculata* are confined to the Lower Cazenovian of the eastern exogeosynclinal sediments, and range throughout the Cazenovian in epeiric deposits to the west. *Phacops rana paucituberculata* is known only from the Upper Cazenovian of Ohio and Michigan. *Phacops rana rana* ranges from the

Middle Cazenovian through the Taghanic (and perhaps Finger Lakes) of the exogeosyncline, but is restricted to the Tioughniogan west of New York and the Appalachians to the south; two specimens of apparent Taghanic age are known from the Cedar Valley Formation of Iowa. *Phacops rana norwoodensis* is known only from the Taghanic. Thus a simple count of dorsoventral files could materially aid the field biostratigrapher working in the Middle Devonian of eastern and central North America.

VARIATION IN *PHACOPS IOWENSIS*

Phacops iowensis is not found abundantly in any formation and was presumably a rare species throughout its history. Originally described from the Cedar Valley of Iowa, its distribution is primarily within the Michigan Basin where it occurs sporadically throughout the Traverse Group.

In sharp contrast to *P. rana*, stability was the main feature of the history of *P. iowensis* throughout the Middle Devonian. Such variation as can be documented is of an order of magnitude less than comparable variation in *P. rana*.

Phacops iowensis specimens never show any deviation from the 13 dorsoventral files present in the earliest known specimen (AMNH 29105) from the Solsville Formation of central New York (fig. 20). The only other record of Marcellus (i.e., Lower Cazenovian) *Phacops* from the native North American lineage occurs in the Ragland sandstone of Alabama. Specimens from the Ragland (USNM 71697) have 14 dorsoventral files and on this basis as well as other criteria are referable to the *P. cristata-pipa* complex of the Eifelian rather than to *P. iowensis sensu stricto*. The origin of the 13 file *P. iowensis* seems to have occurred in much the same manner and at the same time as the reduction from 18 to 17 dorsoventral files occurred in the *P. rana* lineage. *Phacops iowensis* seems to have arisen in the marginal exogeosyncline in the early Cazenovian and to have migrated into the Michigan Basin area with the reinvasion of the Hamilton fauna in Lower Middle Cazenovian times. Indeed, the only subsequent



FIG. 20. Dorsal view of cephalon of *P. iowensis* from the Solsville Member near Morrisville, New York, AMNH locality 3013, AMNH 29105, $\times 2$.

occurrence of *P. iowensis* east of the Michigan Basin proper is in the Hungry Hollow Formation of nearby southwestern Ontario in lowermost Tioughniogan times, and in the Frame Member of the Mahantango Formation at Huntington, Pennsylvania, in the Upper Tioughniogan.

Figure 21 shows the distribution of *P. iowensis* along factor 1 (normalizing by cases) plotted against stratigraphy. Factor components are given in table 4 and sample size and abbreviations in table 5. Although sampling is poor, particularly in post-Cazenovian sediments, it is apparent that there was no change in total lens number per cephalon size throughout the history of *P. iowensis*. As no change in number of dorsoventral files occurred, the number of lenses per dorsoventral file itself remained constant.

Results of the factor analysis of the 26 cephalons of *P. iowensis* where the data were normalized by variables, then by cases, are rather inconclusive and show no easily interpretable, consistent patterns of variation. Discussion of these results will be delayed until the interactions of the two species are considered below.

QUALITATIVE ANALYSIS OF MORPHOLOGY

The facial suture furrow across the ocular platform is invariably strongly developed in *P. iowensis*. However, it is more strongly developed in Tioughniogan and Taghanic specimens than in the Cazenovian specimens from the Alpena and Gravel Point limestones and the Bell shale. Specimens from the basal Tioughniogan Hungry Hollow limestone, however, show only a slight development of the furrow.

The genal angle is invariably more sharply pointed (less rounded) in *P. iowensis* than in *P. rana*. In Cazenovian samples of *P. iowensis*, the genal angle is situated on the ventral margin of the cephalon when seen in lateral view and the dorsal margin of the visual surface is oriented in the horizontal plane. The genal angle is raised above the ventral margin in Tioughniogan and Taghanic specimens.

Glabellar furrow 1p is variably developed and is less deeply incised mesially in younger

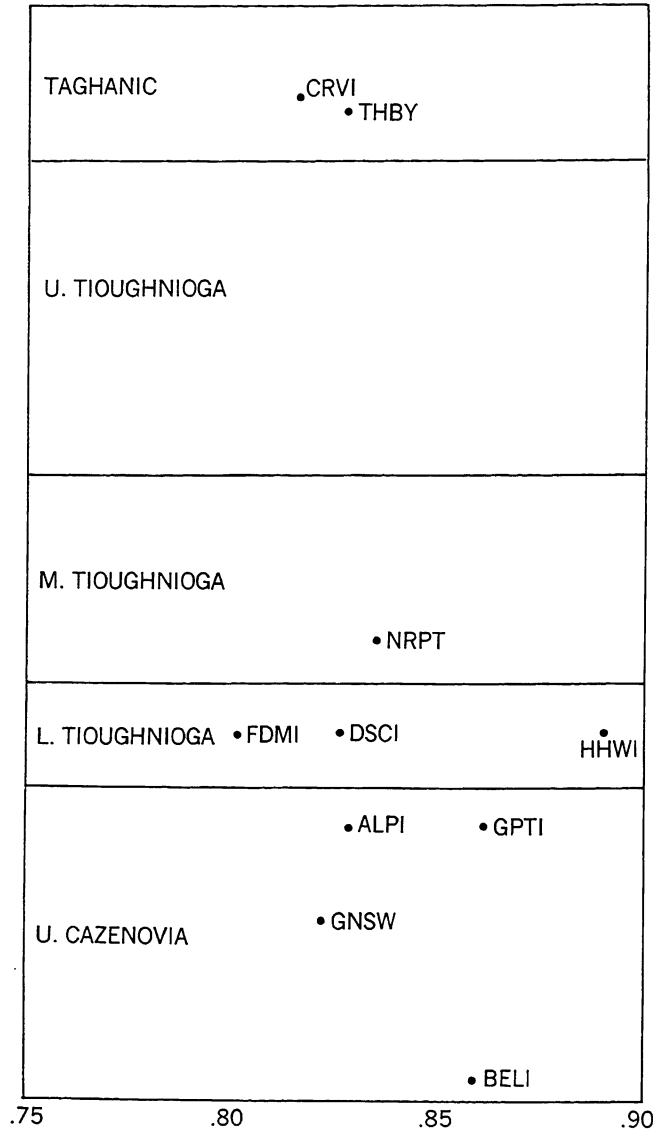


FIG. 21. Factor analysis of *P. iowensis* cephalon. Data normalized by samples. Mean score for each sample for factor 1 (rotated) plotted against approximate stratigraphic position. Sample abbreviations as in table 5. Factor components are given in table 4.

samples. Thus glabellar lobe 1p tends to be better developed in Cazenovian *P. iowensis* than those of the Tioughniogan and Taghanic.

The only conspicuous deviation from the typical *iowensis* pattern of sharp, round tubercles covering the entire surface of the cephalon occurs in a single small sample (USNM 78934),

presumably from the Genshaw Formation near Alpena, Michigan. In this there is a very slight development of transverse elongation of the tubercles on the anterior region of the composite glabellar lobe near the anterior cephalic margin. These specimens are normal *P. iowensis* in all other respects and no other

samples of *P. iowensis* show any signs whatever of flattening and elongation of cephalic tuberculation.

Tubercles covering the entire exoskeleton are not as sharply conical in Cazenovian samples as they are in Tioughniogan and Taghanic specimens of *P. iowensis*.

Pleural furrows are deeply incised in *P. iowensis* and the pleura are rather highly inflated. At least the first two anterior interpleural furrows are developed in most specimens, and occasionally three or four are apparent. The two portions of the fused pleuron separated by the interpleural furrows are of subequal height in Cazenovian *P. iowensis*, but are unequal in younger specimens. The larger section anterior to the interpleural furrow is more highly arched and thus higher than the posterior section in Tioughniogan and Taghanic specimens.

Tubercles cover the entire pygidium and reach the lateral and posterior margins. Tubercles are slightly higher and more conical in Tioughniogan and Taghanic specimens than they are in the Cazenovian specimens.

Tuberculation of the thorax in *P. iowensis* is conservative and similar to that of *P. rana*, with the exception that in *iowensis*, the tubercles never become transversely elongated and flat-

tened on the axial rings. Two specimens from the Hungry Hollow Formation show strong tuberculation along the pleura posterior to the pleural furrow. Tuberculation is usually obsolescent in this area in most specimens of both *P. iowensis* and *P. rana*.

SUBTAXA OF *Phacops iowensis*

The Cazenovian populations of *P. iowensis* form a discrete subunit for which the name *P. iowensis alpenensis* (Stumm) (fig. 22) is available. All post-Cazenovian populations are referable to *P. iowensis iowensis* Delo (fig. 3) except a few rather aberrant specimens from the Lower Tioughniogan (Centerfield) Hungry Hollow Formation, for which the name *P. iowensis southworthi* Stumm (fig. 23) is available. These subspecies are formally diagnosed below.

SYSTEMATIC PALEONTOLOGY

Phacops iowensis alpenensis (Stumm, 1953)

Phacops rana alpenensis STUMM, 1953, p. 139-140, pl. 11.
Phacops rana bellensis STUMM, 1953, p. 139, pl. 10.

Figure 22A-D

EMENDED DIAGNOSIS: Glabellar furrow 1p deeply incised. Tubercles moderately conical over entire exoskeleton. Genal angle near

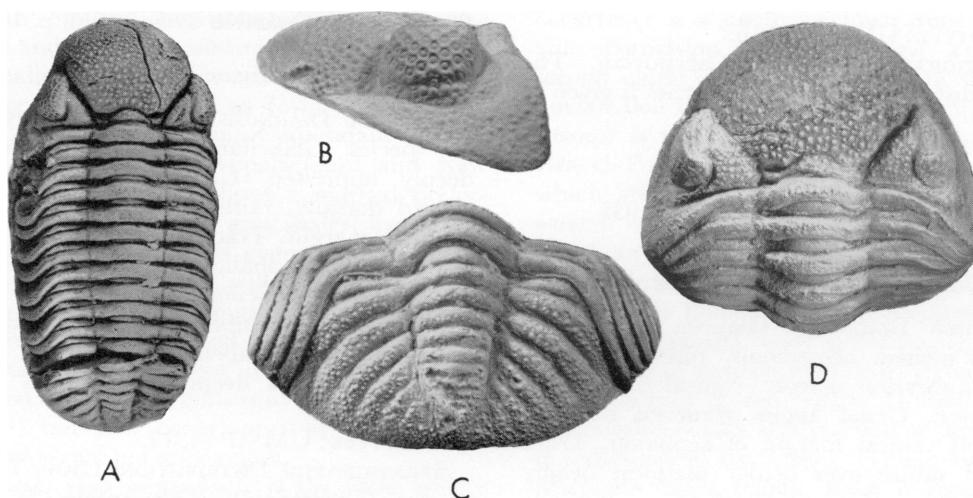


FIG. 22. *Phacops iowensis alpenensis* (Stumm, 1953). A. Dorsal view of holotype, Alpena Formation, UMMP locality 40, UMMP 25516, $\times 1$. B. Left lateral view of cephalon, Alpena Formation, UMMP locality 53, UMMP 29628, cast of paratype, Buffalo Museum of Science E 15211, $\times 2$. C. Dorsal view of paratype pygidium, same horizon and locality as B, UMMP 29559, $\times 2$. D. Dorsal view of cephalon of enrolled specimen, Alpena Formation, AMNH locality 3059, AMNH 28895, $\times 2$.

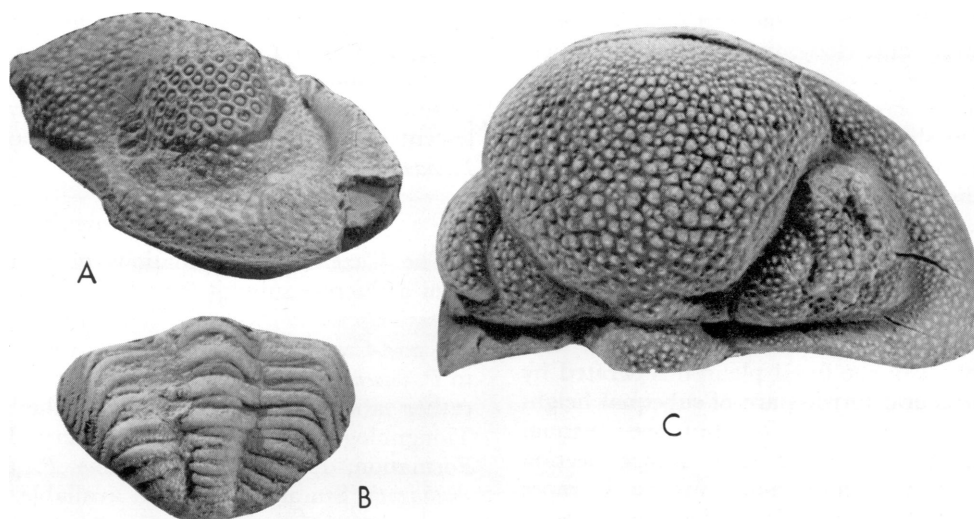


FIG. 23. *Phacops iowensis southworthi* Stumm, 1953. Hungry Hollow Formation, UMMP locality B. A. Left lateral view of cephalon, UMMP 24306, $\times 2$. B. Pygidium and posterior portion of thorax, UMMP 25450, $\times 1$. C. Dorsal view of cephalon of holotype, UMMP 24313, $\times 2$. See also figure 24.

ventral margin of cephalon, less steeply recurved than in other subspecies. Trace of facial suture over ocular platform moderately deeply incised.

Pleural furrows only moderately deeply incised and pleura moderately arched for species.

HOLOTYPE: UMMP 25516.

STRATIGRAPHIC RANGE: Cazenovian. The precise distribution of this subspecies is given in table 8.

Phacops iowensis iowensis Delo, 1935

Figure 3A-C

See Diagnosis of species for synonymy.

EMENDED DIAGNOSIS: Glabella furrow 1p variably incised, occasionally obsolescent medially. Tubercles sharply conical over entire exoskeleton. Genal angles recurved dorsally, raised off ventral margin of cephalon. Trace of facial suture over ocular platform deeply incised.

Pleural furrows deeply incised; pleura highly arched.

HOLOTYPE: SUI 9-266.

STRATIGRAPHIC RANGE: Tioughniogan, Taghanic. Distribution of this subspecies is summarized in table 8.

Phacops iowensis southworthi Stumm, 1953

Phacops iowensis southworthi STUMM, 1953, p. 141-142, pl. 12.

Figure 23A-C

EMENDED DIAGNOSIS: Exoskeleton very large for species. Glabellar furrow 1p moderately deeply impressed. Genal angle slightly recurved dorsally, raised slightly above ventral cephalic margin. Trace of facial suture across ocular platform shallow for the species. Tubercles on exoskeleton large, sharply conical. Numerous small tubercles interspersed with large tubercles on glabella.

Pleural furrows deeply incised and pleura highly arched.

HOLOTYPE: UMMP 24313.

STRATIGRAPHIC DISTRIBUTION: Lower Tioughniogan (Centerfield). This species is based solely on specimens from the Hungry Hollow Formation of southwestern Ontario.

INTERACTIONS BETWEEN *PHACOPS RANA* AND *PHACOPS IOWENSIS*

SUMMARY OF THE DISTRIBUTION OF THE TWO SPECIES

ALTHOUGH THE DISTRIBUTIONS of *P. rana* and *P. iowensis* have been discussed in the previous two chapters in conjunction with interpopulational variation, their distributions are briefly clarified and summarized here and tabulated in table 8.

Phacops rana

Phacops rana crassituberculata first appears as isolated occurrences in the Lower Cazenovian Delaware and Dundee limestones of Ohio and the Solsville siltstone of east-central New York. This subspecies and *P. rana milleri* are nearly ubiquitous higher in the Cazenovian and show a marked preference for calcareous shales. *Phacops rana paucituberculata* is known only from the Cazenovian Plum Brook shale of north-central Ohio and as a single specimen from the Cazenovian Upper Ferron Point shale of north-eastern Michigan.

Phacops rana rana first appears in the Middle Cazenovian of western New York in the argillaceous Stafford limestone, replaces *P. rana milleri* and *P. rana crassituberculata* in the east, and gradually spreads westward. Although *P. rana rana* occurs as far west as Iowa and adjacent states, it is perhaps most abundant in the Tioughniogan of the Appalachians and New York. This subspecies shows a marked preference for soft calcareous gray shales; any fossiliferous formation of this general facies in the Hamilton of New York will contain specimens of *P. rana rana*. Its distribution in the "encrinal" limestones and silt and sandstones is more erratic. *Phacops rana rana* usually preferred fine-grained, slightly argillaceous calcareous substrates, but rich occurrences in more clastic formations are not uncommon.

Phacops rana norwoodensis is the most widely distributed of the subspecies of *P. rana*. It is found in the calcareous shales and limestones of the Tully Formation and its equivalents westward through Michigan, Wisconsin, and Iowa. Its lack of geographic restrictions reflects the disappearance and presumed extinction of

P. iowensis and the disappearance of *P. rana rana* except in eastern New York and Maryland. A few specimens have been recovered from Frasnian "Chemung" sandstones of New York and Maryland. Although poorly preserved, these specimens seem referable to *P. rana rana*, not to *P. rana norwoodensis*, and simply represent a greatly diminished population near extinction.

Phacops iowensis

Phacops iowensis has been regarded as strictly of Taghanic age, with the exception of *P. iowensis southworthi* of the Hungry Hollow Formation of southwestern Ontario. It is a rather rare species in comparison with *P. rana*. In areas of geographic overlap, *P. iowensis* tends to occur in the purer limestones, and the subspecies of *P. rana* in the shalier units, although there are numerous and important exceptions to this generalization. The actual temporal range of *P. iowensis* is approximately as great as that of *P. rana*. The bulk of the history of *iowensis* was limited to the Michigan Basin. The earliest occurrence is a single specimen from the Solsville Formation of central New York. The second oldest specimen comes from the Cazenovian Bell shale of eastern Michigan. *Phacops iowensis* is most abundant in the Alpena and Gravel Point limestones of Michigan, both of which are upper Cazenovian. *Phacops iowensis iowensis* is found rarely in the Dock Street Clay and Four Mile Dam Formation, and is present as a single known specimen from the Tioughniogan Norway Point Formation of eastern Michigan. It also occurs rarely in the Lower Petoskey Formation of western Michigan. Its subsequent disappearance in the central United States is attributable to lack of deposition or preservation of sediments in the Upper Tioughnioga of the Michigan Basin region, since it reappears in some units of the Cedar Valley Formation as well as in the Potter Farm and Thunderbay limestones of eastern Michigan. A single pygidium from the Frame shale (AMNH loc. 3072) in Pennsylvania is the only known Upper Tioughniogan occurrence of *P. iowensis*.

TABLE 8
DISTRIBUTION OF THE SUBSPECIES OF *Phacops rana* AND *Phacops iowensis*

Formation	Prc	Prm	Prp	Prr	Prn	Pia	Pis	Pii
Central New York								
"Chemung"	—	—	—	X	—	—	—	—
Tully	—	—	—	X ^a	X ^a	—	—	—
Cooperstown	—	—	—	X	—	—	—	—
Portland Point	—	—	—	X	—	—	—	—
Panther Mountain	—	—	—	X	—	—	—	—
Stone Mill	—	—	—	X	—	—	—	—
Butternut	—	—	—	X	—	—	—	—
Pompey	—	—	—	X	—	—	—	—
Delphi Station	—	—	—	—	—	—	—	—
Mottville	—	—	—	—	—	—	—	—
Cardiff (Solsville)	X ^a	—	—	X ^a	—	X	—	—
Western New York								
Windom	—	—	—	X	—	—	—	—
Kashong	—	—	—	X	—	—	—	—
Menteth	—	—	—	X	—	—	—	—
Deep Run	—	—	—	X	—	—	—	—
Tichenor	—	—	—	X	—	—	—	—
Wanakah	—	—	—	X	—	—	—	—
Ledyard	—	—	—	X	—	—	—	—
Centerfield	—	—	—	X	—	—	—	—
Levanna	—	—	—	X	—	—	—	—
Stafford	—	—	—	X	—	—	—	—
Oatka Creek	—	—	—	?	—	—	—	—
Southwestern Ontario								
Widder	—	—	—	X	—	—	—	—
Hungry Hollow (Coral M.)	—	—	—	X	—	—	X	—
Hungry Hollow (Ls. M.)	—	—	—	X	—	—	X	—
Arkona (U.)	—	X	—	—	—	—	—	—
Arkona (L.)	X	—	—	—	—	—	—	—
Northeastern Michigan								
Thunderbay	—	—	—	—	—	—	—	X
Potter Farm	—	—	—	—	—	—	—	X
Norway Point	—	—	—	—	—	—	—	X
Four Mile Dam	—	—	—	—	—	—	—	X
Dock Street	—	—	—	X	—	—	—	X
Alpena	—	—	—	—	—	X	—	—
Newton Creek	—	—	—	—	—	—	—	—
Upper Genshaw	—	?	—	—	—	X	—	—
Lower Genshaw	—	X	—	—	—	X	—	—
Upper Ferron Point	—	X	X	—	—	—	—	—
Lower Ferron Point	X	—	—	—	—	—	—	—
Rockport Quarry (basal 18")	—	X	—	—	—	—	—	—
Bell	—	X	—	—	—	X	—	—
Rogers City	—	—	—	—	—	—	—	—
Dundee	—	—	—	—	—	—	—	—
Northwestern Michigan								
Upper Petoskey	—	—	—	—	X	—	—	—
Lower Petoskey	—	—	—	—	—	—	—	X
Upper Charlevoix	—	—	—	—	—	—	—	?
Gravel Point (<i>emmetensis</i> zone)	—	—	—	X	—	X	—	—
Lower Gravel Point	—	—	—	—	—	X	—	—

TABLE 8—(Continued)

Formation	Prc	Prm	Prp	Prr	Prn	Pia	Pis	Pii
Northwestern Michigan								
Ten Mile Creek	—	—	—	X	—	—	—	—
Upper Silica	X	X	—	—	—	—	—	—
Lower Silica (with <i>Paraspirifer</i>)	X	X	—	—	—	—	—	—
Dundee	X	—	—	—	—	—	—	—
North-central Ohio								
Prout	—	—	—	?	—	—	—	—
Plum Brook	—	—	X	—	—	—	—	—
Delaware	X	—	—	—	—	—	—	—
Eastern Wisconsin								
Milwaukee (Zones B, C)	—	—	—	—	X	—	—	—
Northeastern Iowa and Northwestern Illinois								
Coralville	—	—	—	—	X	—	—	—
Rapid	—	—	—	—	X	—	—	—
Solon	—	—	—	?	?	—	—	X
Wapsipinicon	—	—	—	—	—	—	—	—
Southwestern Illinois								
Saint Laurent (basal 10')	X	—	—	—	—	—	—	—
Southern Indiana								
Beechwood	—	—	—	?	—	—	—	—
Swanville	—	—	—	—	—	—	—	—
Silver Creek	—	X	—	—	—	—	—	—
Deputy	—	X	—	—	—	—	—	—
Speeds	—	—	—	—	—	—	—	—
Maryland, Virginia, West Virginia								
"Chemung"	—	—	—	?	—	—	—	—
Harrell	—	—	—	?	—	—	—	—
Upper Romney	—	—	—	X	—	—	—	—
Lower Romney	—	X	—	—	—	—	—	—
South-central Pennsylvania								
Tully Member of the Harrell Formation	—	—	—	?	—	—	—	—
Upper Shale (Frame)	—	—	—	X	—	—	—	X
Montebello	—	—	—	—	—	—	—	—
Lower Shale	—	—	—	—	—	—	—	—
Eastern Pennsylvania								
"Tully"	—	—	—	?	—	—	—	—
Upper Mahantango	—	—	—	X	—	—	—	—
"Centerfield"	—	—	—	X	—	—	—	—
Lower Mahantango	—	—	—	X	—	—	—	—
Alabama								
Ragland	—	—	—	—	—	?	—	—

Key: Prc *Phacops rana crassituberculata*; Prm, *Phacops rana milleri*; Prp, *Phacops rana paucituberculata*; Prr, *Phacops rana rana*; Prn, *Phacops rana norwoodensis*; Pia, *Phacops iowensis alpenensis*; Pis, *Phacops iowensis southworthi*; Pii, *Phacops iowensis iowensis*. ^a variable population (see text). X, present in formation. ?, probably present in formation.

MUTUAL OCCURRENCE OF *PHACOPS* *RANA* AND *PHACOPS IOWENSIS*

Although there is a broad overlap in both the geographic and time distributions of *P. rana* and *P. iowensis*, the two almost never coexisted. The Hungry Hollow Formation of southwestern Ontario has yielded many specimens of *P. rana*

and only a few isolated tagmata of *P. iowensis*, but one specimen from the University of Michigan Museum of Paleontology shows a cephalon of *P. iowensis southworthi* actually touching a cephalon of *P. rana rana* on the same bedding plane (fig. 24). This specimen is the only direct evidence for coexistence of the two species.



FIG. 24. Slab from Coral Member, Hungry Hollow Formation, UMMP locality B, showing association of two cephalons of *Phacops rana rana* with a cephalon of *Phacops iowensis southworthi* on the same bedding plane. The upper two specimens are *rana*; the lower cephalon is the holotype of *southworthi*. UMMP 24313, $\times 1.5$. See also figure 4C and 23C.

TABLE 9

FORMATIONS IN WHICH BOTH *Phacops rana* AND *Phacops iowensis* OCCUR

Formation	Prc	Prm	Prr	Pia	Pis	Pii
Dock St. Clay	—	—	R	—	—	R
Gravel Point						
<i>emmetensis</i> Z.	—	—	R	A	—	—
Genshaw	—	A	—	R	—	—
Bell	—	A	—	R	—	—
Hungry Hollow	—	—	A	—	R	—
Solsville	R	—	—	R	—	—
Frame	—	—	A	—	—	R
(Upper Mahantango)						

KEY: Prc, *Phacops rana crassituberculata*; Prm, *Phacops rana milleri*; Prr, *Phacops rana rana*; Pia, *Phacops iowensis alpenensis*; Pis, *Phacops iowensis southworthi*; Pii, *Phacops iowensis iowensis*; A, subspecies relatively abundant; R, subspecies relatively rare.

Table 9 lists all additional formations in which both species are found. In most formations, one species heavily outnumbers the other. Formations such as the Alpena limestone and Gravel Point limestone are rather thick sequences with several subunits readily recognized on lithologic and faunal criteria; no distinction of subunits was made in the majority of museum collections studied, and there is no direct evidence for coexistence in these few formations which have produced both species.

There is no doubt that marine connections for faunal migration existed between the present-day areas of outcrop of Middle Devonian rocks from Iowa to New York. Such connections were probably more widespread than paleogeographic maps have traditionally shown. An example is the occurrence of *P. rana crassituberculata* in the Cazenovian of southwestern Illinois, and the occurrence of a single large specimen of *P. rana milleri* found in float material at Shellsburg, Iowa, earlier this century.

A complete locality list is included as Appendix 2.

INTERACTIONS BETWEEN THE SPECIES

The virtually complete nonoverlap in occurrence of the two species is strongly indicative of mutual exclusion. Although it is to some degree true that, within the Michigan Basin, *P. iowensis* occurs in the purer limestones, whereas *P. rana* is most commonly found in more argillaceous units. *P. rana* is found in pure, dense limestones throughout the Middle Devonian outside the geographic distribution range of *P. iowensis*. It may be hypothesized that the two species shared too many aspects of their ecology in common to allow them to live sympatrically.

When closely related species with essentially similar ecological requirements and modes of life become sympatric, one species will either resorb the other, or competitively exclude the other, or a mutual subdivision of the range of variation of one or more ecological parameters will result, allowing coexistence to continue. In the one seemingly valid instance of coexistence of *rana* and *iowensis* (in the Hungry Hollow Formation, fig. 24), *rana* is a typical *P. rana rana* with 17 dorsoventral files. All the other qualitative features of the morphology of these *rana* seem well within the range of variation of other Centerfield *rana*. *Phacops iowensis* is known from three cephalons, two pygidia, and one thorax from

the Hungry Hollow; all of these specimens are in the collections of the Museum of Paleontology of the University of Michigan (UMMP 24306, 25450, and 24313). They differ from other *P. iowensis* in a variety of ways and are very large compared to the normal maximum size seen in other populations. This suite of specimens forms the hypodigm of the subspecies *P. iowensis southworthi*.

Hybridization upon sympatric occurrence of the two species would have been very unlikely in view of the probable separate ancestries of the two species. Subdivision of ecological realms in sympatric situations frequently results in "character displacement," essentially an emphasis of some of the morphological differences between the species. Most discussions of character displacement deal with features directly related to subdivision of specific ecological

parameters (e.g., Lack, 1947, on bill morphology in relation to seed size in birds). Unfortunately, the adaptive significance of most of the morphological features in *Phacops* are unknown. But though the *rana* of Hungry Hollow appear "normal," *P. iowensis southworthi* is far more dissimilar to typical *rana* morphology than are any other *iowensis* specimens known. *Phacops iowensis* in the Four Mile Dam and Dock Street Formations (correlatives of the Hungry Hollow in eastern Michigan) are much more typical of the species in over-all appearance and more similar to *rana* than are the *P. iowensis southworthi* specimens.

Factor analysis clarifies the relationships between the two species considerably. In rotated factor 1, in which the data were normalized by cases, figure 25 shows the distributions of both species simultaneously plotted strati-

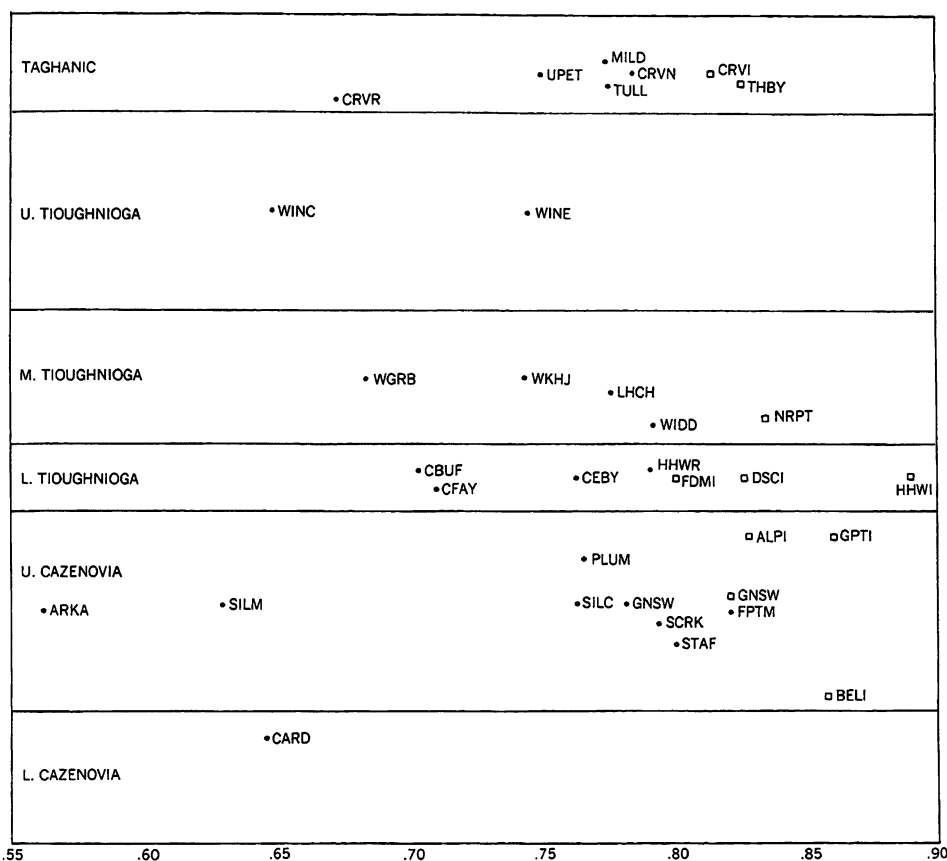


FIG. 25. Factor analysis of *P. iowensis* (□) and *P. rana* (.) cephalae. Data normalized by samples. Mean score for each sample for factor 1 (rotated) plotted against approximate stratigraphic position. Sample abbreviations as in table 5. Factor components are given in table 4.

graphically. Cazenovian *P. iowensis* are relatively close to the main line of *P. rana* in terms of lens number per cephalon size, although *iowensis* generally has even fewer lenses per cephalon size than the extreme condition in *P. rana*. Whereas *P. rana* shows its variation toward increase in number of lenses per cephalon size, *iowensis* remains relatively constant. The one cephalon of *P. iowensis southworthi* sufficiently well preserved to be measured is shown on the plot (fig. 25). As expected, *southworthi* shows the highest loading of all *iowensis* on factor 1, corroborating the hypothesis of character displacement to a certain extent. Perhaps of greater interest is the fact that HHWR and WIDD are closer to the average *iowensis* than any other post-Lower-Middle Cazenovian *rana* population.

It is to be remembered that WIDD is here thought to be misidentified and actually comes from the Hungry Hollow. In terms of lens number per cephalon size, *rana* from Hungry Hollow seems to be actually convergent on *iowensis*. According to factor 1, then, the picture does not seem to be one of classic, mutual divergence of sympatric individuals of two species, but convergence of one (*rana*) toward the other (*iowensis*) and consequent responsive divergence of *iowensis* away from general *rana* morphology. Although the general trend of increase in lens number per cephalon size in *P. rana* is away (i.e., divergent) from *iowensis*, *P. rana norwoodensis* from the Taghanic reconverge on *iowensis* in this respect. Reduction of number of dorsoventral files from 18 to 15 within the *rana*

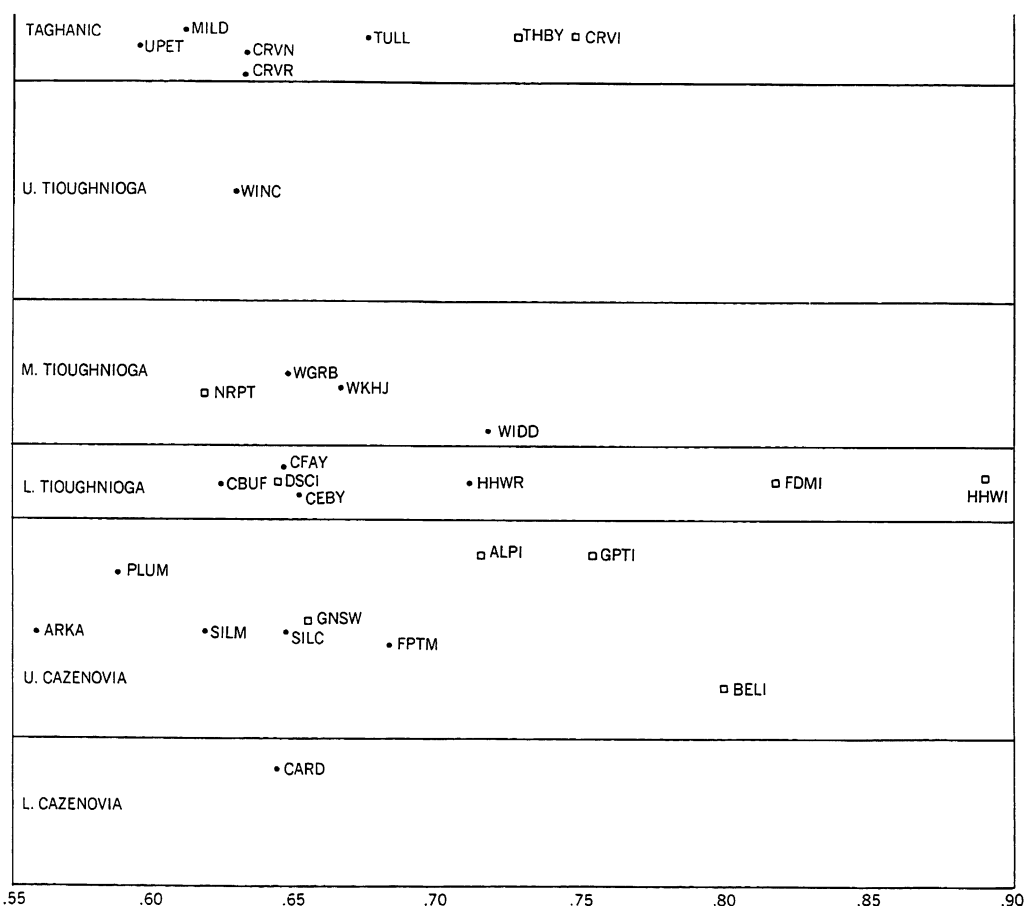


FIG. 26. Factor analysis of *P. iowensis* (□) and *P. rana* (.) cephalae. Data normalized by variables, then by cases. Mean score for each sample for factor 2 (rotated) plotted against approximate stratigraphic position. Sample abbreviations as in table 5. Factor components are given in table 6.

lineage, of course, amounts to a partial convergence on the *iowensis* condition of 13 dorso-ventral files.

Communalities in a factor analysis where the data were normalized by variables are proportional to the over-all size of each specimen. Although not illustrated, these communalities show that throughout the stratigraphic range, all specimens of *P. iowensis* fall within the variation in size of *P. rana*, with the sole exception of one very large specimen of *P. iowensis southworthi* included in the analysis.

Simultaneous plots of *P. rana* and *P. iowensis* scores for the factor analysis where the data were normalized by variables, then by cases, are presented in figures 26, 27, and 28. Factor 2, based primarily on variation in LOP, is shown in figure 26; here again, APPM, APPR,

LHCH, SCRK, STAF, and WINE are omitted because they consist of internal molds. As in the case of factor 1, in which the data were normalized by cases only, WIDD and HHWR have the highest scores of any *P. rana* sample and actually fall close to the grand mean score of *P. iowensis*. HHWI (*P. iowensis southworthi*) is again displaced farther away from *rana* than any other *P. iowensis* sample, although specimens from the Four Mile Dam limestone also score high. The pattern is thus repeated: *P. iowensis southworthi* seems to be "rebounding" away from *P. rana*, and samples of *P. rana* assumed to be sympatric are converging on *P. iowensis*.

Factor 3 (fig. 27) shows a somewhat different pattern. Based on eye height, HHWI again falls at one end of the extreme of variation in *P. iowensis*, farthest away from *P. rana*. Among all

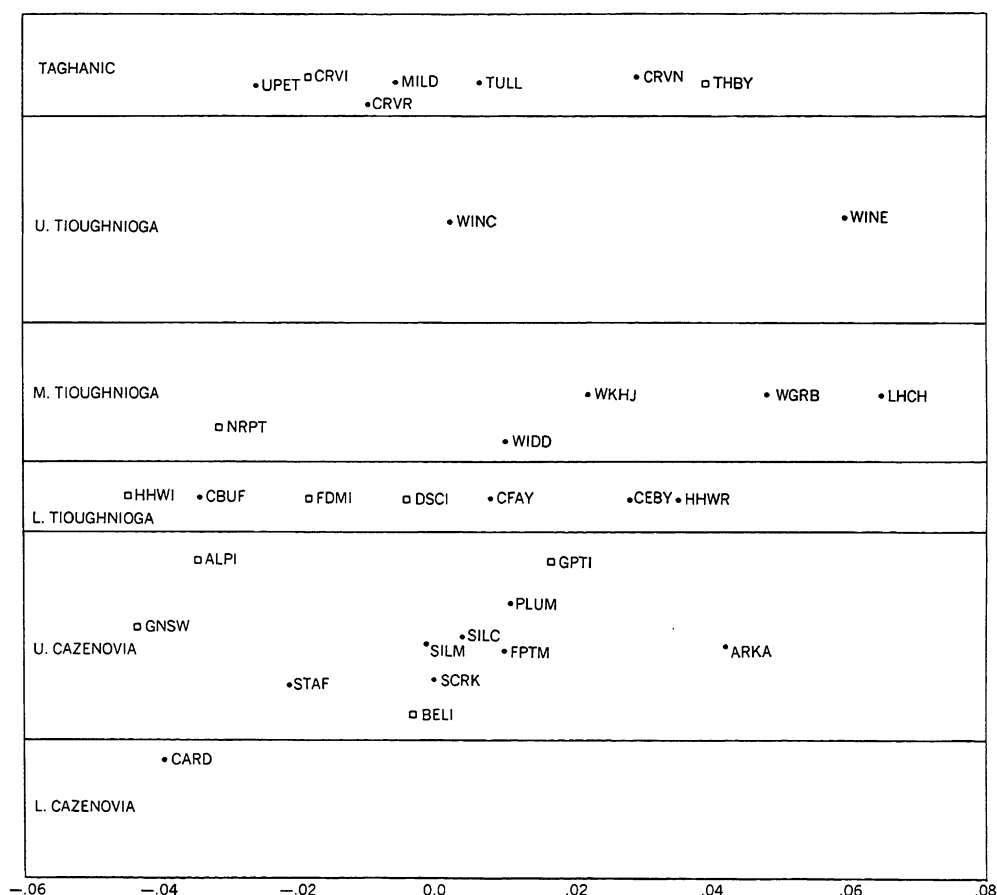


FIG. 27. Factor analysis of *P. iowensis* (□) and *P. rana* (•) cephalae. Data normalized by variables, then by cases. Mean score for each sample for factor 3 (rotated) plotted against approximate stratigraphic position. Sample abbreviations as in table 5. Factor components are given in table 6.

samples of *P. rana* from Centerfield limestone equivalents, however, Hungry Hollow *P. rana* score farthest from *P. iowensis*. Here the scores of HHWR and WIDD are not identical. There is thus some evidence for a more classic picture of character displacement involving eye height between these two assumed sympatric populations.

Factor 4 (fig. 28), involving proportions of glabellar lengths, widths, and eye complex size, shows no peculiarities in the scores of either HHWI or HHWR and seems not to be involved in the interactions of the two species in the Hungry Hollow.

The interrelationships between the only populations of the two species known to have coexisted are therefore complex. The small *southworthi* sample shows particularly strong divergence from *rana* in the following characteristics:

1. Normal *iowensis* tuberculation is developed to an extreme, where very large conical tubercles cover the entire surface of the carapace.

2. The few known specimens of *southworthi* are very much larger than any other known specimen of *iowensis*. This accounts in large measure for the divergence in lens number per cephalon size of *P. iowensis southworthi* from the normal *rana* condition.

3. *P. iowensis southworthi* shows a relatively shorter (lengthwise) and taller visual surface (factors 2 and 3, normalized by variables, then by cases) than is usual for *iowensis*.

P. iowensis southworthi shows no apparent convergence toward *P. rana* in any respect.

Specimens of *P. rana* from the Hungry Hollow Formation show convergence on *iowensis* in the following characteristics:

1. Smaller number of lenses per cephalon size than is usual for the species in Centerfield times.

2. Larger posterior length of the ocular platform and concomitant shorter eye length than is usual for *P. rana* of Centerfield age.

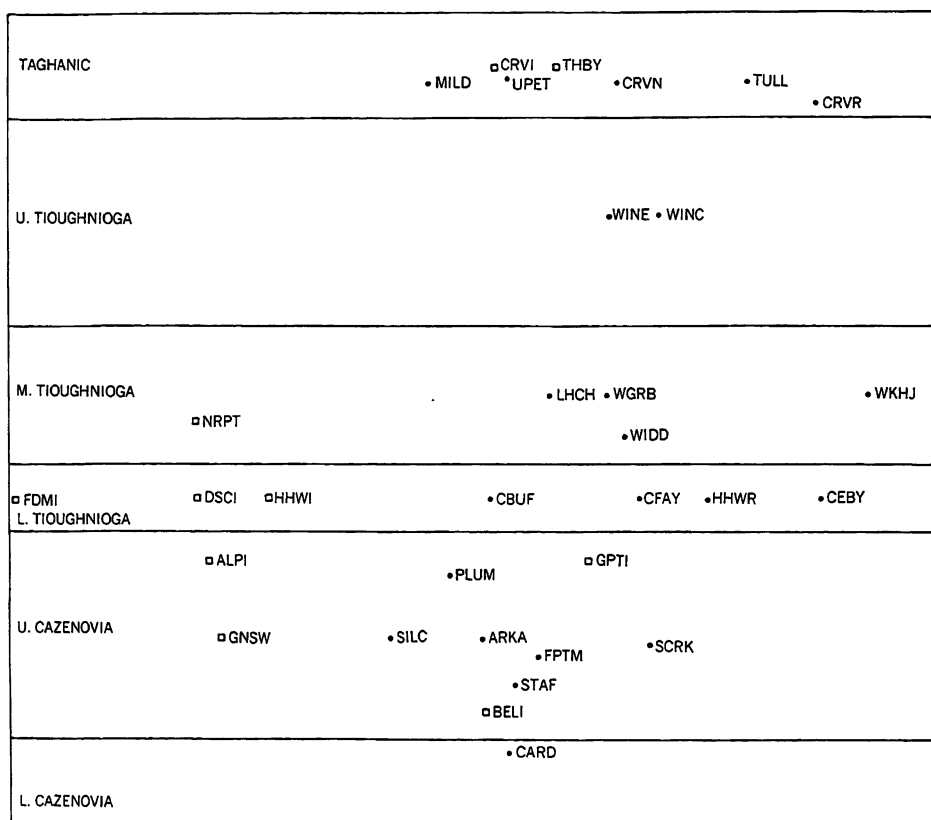


FIG. 28. Factor analysis of *P. iowensis* (□) and *P. rana* (•) cephalon. Data normalized by variables, then by cases. Mean score for each sample for factor 4 (rotated) plotted against approximate stratigraphic position. Sample abbreviations as in table 5. Factor components are given in table 6.

Phacops rana from Hungry Hollow show no change from normal *P. rana rana* of Centerfield age in having:

1. Seventeen dorsoventral files.
2. Normal ornamentation.

Phacops rana from Hungry Hollow show divergence from *iowensis* in the following:

1. Narrower cephalon and shorter visual surface height than in other *P. rana* of Centerfield age (factor 3).

Coexistence, then, produced obvious effects in the morphology of the two species. In general, *rana* tended to converge on, perhaps even to mimic, *P. iowensis*. *Phacops iowensis* tended to accentuate the differences already established between the species. But in other respects, a more classical picture of character displacement is shown by the divergence of the two species.

In terms of over-all phylogenetic history of the two species, factor analysis revealed several instances of trends in *rana* which varied in direction vis à vis *iowensis*. Divergence simply reflects independent histories of the species living in different geographic areas at any one time. Evolutionary changes in one stock for the most part may have had little to do with changes in the other stock, at least through the Cazenovian and Tioughniogan. However, the convergence of *P. rana norwoodensis* in the Taghanic on *P. iowensis iowensis* as seen in factor 1 (normalizing by cases) and factors 3 and 4 (normalizing by variables) is strengthened by convergences in qualitative morphological features. This close resemblance between *norwoodensis* and *iowensis* therefore may not have been wholly fortuitous. Aside from the convergences seen in factor analysis, *norwoodensis* is similar to *iowensis* in the following details, most of which are not applicable to the variable *norwoodensis* population of the Tully limestone:

1. The facial suture furrow of the ocular platform is more deeply incised than in normal *P. rana rana*.
2. Flattening and transverse elongation of tubercles is reduced to the extreme anterior edge of the composite glabellar lobe and posterior row on the occipital lobe.
3. Tuberculation is denser and tubercles are generally smaller and taller and subconical.
4. The pygidium is covered more densely with tubercles which often reach the lateral and posterior margins.
5. The pleura become more highly arched in

conjunction with deeper incision of the pleural furrows.

6. *Phacops rana norwoodensis* has fewest (15) number of dorsoventral files and is thus closer to *P. iowensis* in that respect than any other subspecies of *P. rana* (except *P. r. paucituberculata*).

This list of characters essentially repeats the list of differentia that serve to define the various subspecies of *P. rana*. In other words, the very characters that serve to distinguish *P. rana* from *P. iowensis* are also those that show the greatest amount of variation among various samples of *P. rana*. The character states considered advanced in *P. rana* are closest to the condition exhibited in the (generally) stable *P. iowensis* group. It seems likely, then, that the phylogenetic changes in character states noted in the history of *P. rana* stem from a general over-all "interaction" with *P. iowensis*, and that far from being a stochastic series of adjustments, e.g., to local edaphic conditions, *P. rana* actually converged on *P. iowensis*. It is concluded that the various trends exhibited by *P. rana* represent neither "gradual improvement" nor a guiding "orthoselection" principle controlling adjustment to local edaphic conditions, but an actual morphological (and presumably ecological-ethological) convergence on *P. iowensis* for some unknown set of adaptive reasons.

It may further be concluded that the initial assumption that *P. rana* and *P. iowensis* in fact were true "biospecies" was not premature. Their apparently interwoven histories can best be interpreted if this assumption is made, and there seems no reason, in retrospect, to challenge this characterization of the two taxa.

Phacops rana norwoodensis replaces *P. iowensis iowensis* in the Cedar Valley Group and in the Petoskey Formation, so that the only definite Upper Taghanic occurrence of *P. iowensis* is in the Thunderbay and Potter Farm formations of eastern Michigan, where no *rana* are known. It is quite possible that the convergence of *rana* on *iowensis* in Upper Tioughniogan and Taghanic times had much to do with the disappearance (possibly eradication) of *iowensis* in the Taghanic from all but a small portion of its range in the uppermost Tioughniogan and possibly Lower Taghanic.

If the broad conclusions reached on the interactions between *P. rana* and *P. iowensis* are substantially correct as presented above, further light is thrown on the one specific instance

thought to involve character displacement. The apparent case of character displacement involving samples of *P. rana* and *P. iowensis* from the Hungry Hollow Formation is actually very complex and is best viewed as a part of the total history of the interactions between the two species. The reasons why *P. rana rana* from the Hungry Hollow converges on *P. iowensis* in certain respects and diverges or remains "neutral" in others, are only interpretable in the context of previous and subsequent evolutionary changes within the *P. rana* lineage. At least in this instance, the precise nature of the character

displacement depends to a degree on the position of the relevant population within the evolutionary history of its own species, as well as it depends on the interactions with the other species at the particular moment. Although character displacement is largely a phenomenon of sympatry, present results indicate that the full explanation for any particular case must include the previous and subsequent histories of the lineages involved and the general nature of the interactions between the lineages throughout their entire histories.

SUMMARY

TWO TRILOBITE SPECIES, *Phacops rana* (Green, 1832) and *P. iowensis* Delo, 1935 from the Middle Devonian (Cazenovian, Tioughniogan, Taghanic, and ?Finger Lakes) of eastern and central North America, are analyzed in the present study. Other species of *Phacops* previously described from these rocks, including *P. cacapona* Hall, *P. nupera* Hall, and *P. ohioensis*, are considered invalid.

Several largely invariant, nonoverlapping morphological characters serve to differentiate *P. rana* from *P. iowensis*:

1. *P. iowensis* invariably has 13 dorsoventral files, whereas *P. rana* has from 15 to 18.

2. The fixigenal and librigenal moieties of the ocular platform are more sharply defined in *iowensis* than in *rana*.

3. Tubercles in *iowensis* are generally rounded at the base and subconical, whereas those in *rana* are usually bluntly rounded on top. *Phacops rana* shows elongation and flattening of cephalic tubercles on the anterior margin of the composite glabellar lobe, on the margins of the genae, and on the occipital lobe, as well as on the entire axis of the thorax and pygidium. No such flattening and elongation is developed in *P. iowensis*.

4. The lp glabellar furrow is commonly obsolescent mesially in *P. iowensis* and always sharply incised in *P. rana*.

5. The genal angle in *iowensis* terminates in a moderately sharp point, but is generally bluntly rounded in *rana*.

6. Interpleural furrows are more extensively developed on the pygidium of *iowensis* than they are in *rana*.

Phacops rana is morphologically closest to *P. schlotheimi* of the Eifelian of Europe and Africa and probably migrated to Devonian North America along with *Greenops* (*Greenops*) *boothi* (Green) in the Lower Cazenovian (Lower Givetian). *Phacops iowensis* apparently evolved from native North American species of *Phacops* of the Lower and Lower Middle Devonian.

Post-larval growth in *Phacops* is linear and usually adequately described by the equation for a straight line. Allometry between most variables is negligible, and populations may be compared even when biased in terms of portions

of the ontogenetic sequence represented. The cephalon is basically well "integrated," reflecting its nature as a solid tagma. The ocular complex maintains a degree of independence from the major cluster of gross and axial cephalic dimensions.

Theories of relationship should be based on morphologic (including ontogenetic) data, rather than relative position in a biostratigraphic sequence. Hypotheses of relative degree of common ancestry are more economical statements, and more easily capable of rejection than are hypotheses of ancestral-descendant relationships. However, if biostratigraphic data are in rough accord with a previously established theory of relationships, various aspects of the evolutionary process may be investigated. Among such phenomena discussed here are "trends" (biostratigraphic character gradients), modes of speciation, and interspecific interactions.

The primitive number of dorsoventral files is determined to be 18 in *P. rana*, based on considerations of (1) the condition in *P. schlotheimi*, herein considered the sister species of *P. rana*, and (2) ontogenetic information, particularly that derived from rare samples where the number of dorsoventral files is variable. The 17 dorsoventral file condition is derived (from 18), whereas the 15 dorsoventral file condition is thought to have arisen twice, once directly from the 18 dorsoventral file condition, and once from the 17.

All characters, including linear measurements, shown to be important interpopulational variables, have particular "values" in each of the subspecies. In view of the different biostratigraphic ranges of the subtaxa, all of these important variables in fact possess characteristics of "trends" or "biostratigraphic character gradients." A summary of these trends follows:

- (1) Rounding of the genal angle; (2) deeper incision of the facial suture furrow on the ocular platform, and shift of the librigenal moiety of the ocular platform to a more nearly vertical orientation; (3) decrease in the amount of flattening and degree of transverse elongation of ornamental tubercles on the anterior region of the composite glabellar lobe, occipital lobe,

and genal margins; (4) increase in strength of tuberculation on the thorax and pygidium; (5) deeper incision of pleural furrows on the pygidium; (6) loss of interpleural furrows on the pygidium; (7) reduction of length and height of eye through the Middle Tioughniogan, then subsequent reversal in the Upper Tioughniogan and Taghanic; (8) increase in number of lenses per cephalon size within the 17 dorsoventral file lineage of the Cazenovian and Tioughniogan; (9) reduction in number of dorsoventral files from 18 to 15.

Five subspecies of *P. rana* are recognized. Two subtaxa in the Cazenovian are characterized primarily in having 18 dorsoventral files. *Phacops rana milleri* Stewart, 1927 is distinguished from *P. rana crassituberculata* Stumm, 1953, in having a greater number of lenses per dorsoventral file. Variation in this feature is not encountered in the post-Cazenovian history of *P. rana*. The two subspecies are similar in other respects, and seem actually to represent populations adapted to local edaphic conditions. Recognition of two distinct subtaxa is therefore solely a matter of convenience, and the differences between these two taxa are different in kind from the differences between the other three subspecies recognized herein. *Phacops rana crassituberculata* and *P. rana milleri* are restricted to Cazenovian rocks, and though widely distributed, are more abundant in shales and limestones of the cratonal interior. *Phacops rana paucituberculata*, new subspecies, known from five specimens in the Upper Cazenovian, is similar to *P. rana crassituberculata*, but differs in having only 15 dorsoventral files. *Phacops rana crassituberculata*, *P. rana milleri*, and *P. rana paucituberculata* seem to comprise a closely knit complex that resembles a comparable trivariant subdivision of the Eifelian species, *P. schlotheimi*, in Europe. *Phacops rana rana*, with 17 dorsoventral files, arose in the exogeosyncline in the Cazenovian. Restricted to the exogeosyncline throughout the Cazenovian, *P. rana rana* is the only subspecies of *P. rana* known from Tioughniogan sediments. *Phacops rana rana* may have persisted through the Taghanic in the exogeosyncline, and survived into Finger Lakes time. *Phacops rana norwoodensis* Stumm, 1953 with 15 dorsoventral files, is widespread in the Taghanic. Populations from New York show a transition from 17 to 15 dorsoventral files.

Phacops iowensis was apparently always a

rare species. Although its range (Lower Cazenovian-Taghanic) is virtually the same as that of *P. rana*, *P. iowensis* was far more stable and evolutionarily conservative than was *rana*. *Phacops iowensis* was confined to the immediate vicinity of the Michigan Basin throughout most of its history. It apparently arose in the exogeosyncline from the *P. cristata-pipa* complex of the Eifelian. There was no reduction in dorsoventral files within the *P. iowensis* lineage. Factor analysis revealed no phylogenetic change in lens number per cephalon size. Since the number of dorsoventral files was also constant (13), the number of lenses per dorsoventral file in homologous files was also constant. *Phacops iowensis* showed no significant change when plotted against any of the other factor axes calculated in factor analysis when the data were normalized by variables.

"Trends" in *P. iowensis*:

(1) The trace of the facial suture over the ocular platform becomes more deeply incised through time; (2) the genal angle becomes reflexed dorsally and raised above the ventral cephalic margin; (3) glabellar furrow 1p becomes less deeply incised mesially.

Phacops iowensis southworthi Stumm, 1953, of the basal Tioughniogan of southwestern Ontario, exhibits morphological features distinct from the other subspecies that reflect a geographically based interaction with *P. rana*. *Phacops iowensis alpenensis* (Stumm, 1953) is restricted to the Cazenovian of the Michigan Basin. *Phacops iowensis iowensis* occurs in Tioughniogan and Taghanic rocks of the Michigan Basin, Iowa, and (rarely) Pennsylvania.

Although there is a broad overlap in both the geographic and time distributions of *P. rana* and *P. iowensis*, only one probable instance of sympatry is known. In areas of geographic overlap, *P. iowensis* tends to occur in the purer limestones, whereas *P. rana* shows a preference for more clastic and argillaceous calcareous sediments.

The one possible case of sympatry between *rana* and *iowensis* occurs in the Hungry Hollow Formation of southwestern Ontario. Sympatry seems to have induced readily observed morphological changes in the two species:

Phacops iowensis of the Hungry Hollow shows particularly strong divergence from *rana* in the following characteristics:

(1) Normal *iowensis* tuberculation is developed

to an extreme, where very large conical tubercles cover the entire surface of the exoskeleton; (2) the few known specimens of *iowensis* from Hungry Hollow are very much larger than any other known specimen of *iowensis*. This accounts in large measure for the divergence in lens number per cephalon size of *P. iowensis southworthi* from the *rana* condition. (3) *Phacops iowensis southworthi* shows a relatively shorter (lengthwise) and taller visual surface than is usual for *iowensis*.

Phacops iowensis southworthi shows no convergence toward *P. rana* in any respect except absolute size.

Specimens of *P. rana* from the Hungry Hollow Formation show convergence on *iowensis* in the following characteristics:

(1) Smaller number of lenses per cephalon size than is usual for Centerfield *P. rana*; (2) larger posterior length of the ocular platform (LOP) and concomitant shorter eye length than is usual for *P. rana* of Centerfield age.

Phacops rana from Hungry Hollow are similar to normal *P. rana rana* of Centerfield age in having:

(1) 17 dorsoventral files; (2) normal ornamentation.

Hungry Hollow *rana* diverge from *iowensis* in the following:

(1) Narrower cephalon and shorter visual surface than in other *rana* of Centerfield age.

The *P. rana* lineage as a whole converged on *P. iowensis* in many characteristics, including number of dorsoventral files and many ornamental features. This convergence is also seen

in some of the reference vector plots in factor analysis. The convergence was closest in the Taghanic.

The greater amount of morphological change shown by *P. rana* when compared with *P. iowensis* indicates that evolutionary change is more directly related to extent of geographic distribution (greater in *rana* than in *iowensis*) than to persistence through time (about equal for the two species). The allopatric model, where new character states arise on the periphery of the range of a species, is directly applicable to the history of *P. rana*. Important changes in eye morphology originate in the exogeosyncline to the east, and subsequently spread through the epeiric seas on the cratonal interior. The allopatric mode of speciation or subspeciation probably underlies the "sudden" appearance of many Paleozoic taxa in cratonal sediments. Evolutionary phenomena (e.g., development of clines, character displacement) affecting morphology on the species level as seen in recent organisms are applicable to the analysis of fossil species, particularly those for which large samples with good stratigraphic control are available. The fossil record may be used to clarify certain processes seen on a single time plane. For example, although character displacement is largely a phenomenon of sympatry, the full explanation for any particular case must include the previous and subsequent histories of the lineages involved and the general nature of the interactions between the lineages throughout their entire histories.

APPENDIX 1

GLOSSARY OF MORPHOLOGICAL TERMS

CEPHALON

- Apodemal pit, transverse slit on dorsal surface near distal margins of 1p glabellar and occipital furrows, marking site of apodeme.
- Apodeme, exoskeletal invagination forming rod or ridge on visceral surface for attachment of muscles or ligaments.
- Area under visual surface, vertical area of eye below lens-bearing surface, separated from ocular platform by a shallow furrow.
- Ascending diagonal row, oblique row of lenses on visual surface inclined anterodorsally.
- Axial furrow, groove separating glabella from the fixigena and librigena.
- Axis, median region, including glabella and occipital ring.
- Composite glabellar lobe, large, inflated, roughly pentagonal anterior portion of glabella consisting of a fusion of all glabellar lobes except 1p.
- Descending diagonal row, oblique row of lenses on visual surface inclined anteroventrally.
- Dorsoventral file, vertical column of lenses on visual surface.
- Doublure, reflexed continuation of dorsal exoskeleton as a ventral shelf.
- Eye, large visual organ situated on librigena.
- Facial suture, obsolescent molting suture running transversely from area anterior to genal angle across the ocular platform then anteriorly behind margin of visual surface, connecting at the anterior cephalic margin around front of glabella.
- Fixigena, portion of cephalon between axis and facial suture. Includes palpebral lobe, palpebral area, genal angle, and fixigenal moiety of ocular platform.
- Fixigenal moiety of ocular platform, posterior portion of ocular platform, separated from anterior (librigenal) portion by a groove representing trace of obsolescent facial suture.
- Frontal arch, dorsally convex curvilinear profile of ventral margin of cephalon, when viewed anteriorly.
- Frontal arch sag, ventrally convex sagittal depression sometimes developed in frontal arch.
- Genal angle, posterolateral corner of cephalon.
- Glabella, axial region bounded distally by axial furrows, posteriorly by occipital furrow, and anteriorly by cephalic margin.
- Horizontal row, row of lenses parallel to dorsal and ventral margins of visual surface.
- Librigena, portion of cephalon distal to facial suture. Includes visual surface, area under visual surface, librigenal moiety of ocular platform, and portion of gena anterior or distal to facial suture.
- Librigenal moiety of ocular platform, anterior portion of ocular platform, separated from posterior (fixigenal) portion by a groove representing trace of obsolescent facial suture.
- Occipital furrow, transverse furrow separating occipital lobe from glabella.
- Occipital lobe, posterior axial lobe.
- Ocular platform, flat ridge supporting eye, continuous posteroproximally with palpebral area. Separated posteriorly from cephalic border by shallow posterior border furrow, and from distal portions of gena by a shallow furrow. Bounded dorsally by area under visual surface and divided into fixigenal and librigenal moieties by a transverse groove representing trace of obsolescent facial suture.
- 1p Glabellar furrow, continuous transverse furrow between composite glabellar lobe (anteriorly) and 1p glabellar lobe (posteriorly).
- 1p Glabellar lobe, complete transverse axial segment of glabella anterior to occipital lobe and posterior to composite glabellar lobe.
- Palpebral area, inflated area of fixigena continuous posteroproximally with ocular platform and bounded anteroproximally by axial furrow and distally by palpebral furrow.
- Palpebral furrow, faint distally convex groove separating the palpebral area (prox.) from the palpebral lobe (dist.).
- Palpebral line, imaginary transverse line connecting points of maximum convexity of the palpebral lobes.
- Palpebral lobe, reniform inflated area of fixigena bounded distally by facial suture and proximally by palpebral furrow.
- Posterior border furrow, transverse groove immediately anterior to posterior cephalic margin, continuous with occipital furrow.
- Sclera, interlensar exoskeletal tissue of visual surface.
- Tagma, regionally distinct area of exoskeleton generally consisting of a number of similar segments, each bearing similar appendages.
- 3p Glabellar furrow, anteriormost noncontinuous furrow of composite glabellar lobe consisting of two branches, the anterior one of which runs anterodistally parallel with the axial furrow. The posterior ramus is transverse and situated on the distal portion of the composite glabellar lobe.
- Tubercle, projection of variable size and shape on dorsal surface of exoskeleton.

2p Furrow, noncontinuous transverse furrow of composite glabellar lobe, posterior to 3p glabellar furrow.

Vincular furrow, continuous semicircular groove on doublure just proximal to ventral margin.

Groove is smooth anteriorly and notched posteriorly.

Visual Surface, lens-bearing portion of eye.

HYPOSTOMA

Anterior wing, dorsal extension of anterolateral corners.

(Anterior) wing process, invagination forming a process on the visceral side of the anterior wing.

Central body, inflated central region of hypostoma.

Hypostomal suture, line of junction between anterior edge of hypostoma and posterior margin of frontal cephalic doublure.

THORAX AND PYGIDIUM

Articulating half-ring, crescentic anterior extension of axial ring (anterior ring only on pygidium) which passes under axial ring (or occipital lobe) immediately anterior.

Axial furrow, longitudinal groove separating pleura from axial ring.

Axial ring, central raised portion of tergite bounded distally by axial furrows.

Interpleural Furrow, line of separation of pleura in thorax, becoming very faint or lost in fused pygidial pleura.

Pleural furrow, groove along pleural surface.

Pleuron, lateral portion of thoracic or pygidial segment.

Ring furrow, transverse furrow separating axial rings of pygidium.

APPENDIX 2

LOCALITY LIST

- AMNH
- | | |
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| <p>3013. Solsville Member, Marcellus Formation. Borrow pit in pasture on right side of Swamp Road, 2.6 miles north of Morrisville, New York.</p> <p>3028. ?Pompey Member, Skaneateles Formation. Borrow pit on No. 4 Road just east of junction with Pompey Center Road, Pompey Center, New York.</p> <p>3029. Pompey Member, Skaneateles Formation. Road cut on U. S. Route 20, top of hill west of Pompey Center, New York.</p> <p>3030. Butternut Member, Skaneateles Formation. Borrow pit on secondary road approximately 0.5 mile east of southeastern shore of Lake Moraine, Madison County, New York.</p> <p>3031. Ludlowville Formation. Borrow pit near Hatch's Lake, at intersection of Bradley Brook and Soule roads, 3.6 miles south of intersection of Bradley Brook Road and N. Y. 26, near Eaton, New York.</p> <p>3032. Lower Ludlowville (including Stone Mill limestone). Robert's Road Quarry, north of N. Y. 26 on Robert's Road, West Eaton, New York.</p> <p>3033. Lower Centerfield Member, Skaneateles or Ludlowville Formation. Fayette Town Quarry, 0.25 mile west of Fayette, New York.</p> <p>3034. Cooperstown Member, Moscow Formation. Borrow pit in New York State-owned land on dirt road approximately 1 mile east of loc. 3035.</p> <p>3035. Cooperstown Member, Moscow Formation. Borrow pit off Deep Spring Road, 1.3 miles from intersection of Deep Spring Road with Lebanon Road, south of Lebanon, New York.</p> <p>3036. Windom Member, Moscow Formation. 1.3 miles west of N. Y. 80 on Kingsley Road (intersection of Kingsley Road with N. Y. 80 is 1.0 mile south of loc. 3037).</p> <p>3037. Portland Point Member, Moscow Formation. Road cut on N. Y. 80, 0.8 mile south of intersection of N. Y. 80 and U. S. 20.</p> <p>3038. Windom Member, Moscow Formation. Portland Point Quarry, 1 mile southwest of South Lansing, New York.</p> <p>3039. Tully Formation. Same as loc. 3038.</p> <p>3040. Tully Formation. Carpenter Road, 1 mile from "T" intersection with N. Y. 80, south of Sheds, New York.</p> <p>3041. Wanakah Member, Ludlowville Formation.</p> | <p>Jaycox Run, 0.25 mile west of N. Y. 39, 6.5 miles south of Avon, New York.</p> <p>3042. Deep Run Member, Ludlowville Formation. Same as loc. 3041.</p> <p>3043. Menteth Member, Moscow Formation. Same as loc. 3041.</p> <p>3044. Centerfield Member, Ludlowville Formation. Cut along tracks of Delaware and Western Railroad, 3 miles west of East Bethany, New York, near Francis road.</p> <p>3045. Ledyard-Wanakah Members, Ludlowville Formation. Same as loc. 3044.</p> <p>3046. Stafford Member, Skaneateles Formation. Buffalo Creek east of intersection of Indian Church and Mineral Spring Roads, Buffalo, New York.</p> <p>3047. Centerfield Member, Ludlowville Formation. Buffalo Creek, near Blossom, New York.</p> <p>3048. Wanakah Member, Ludlowville Formation. Cazenovia Creek near Transit Road, Erie County, New York.</p> <p>3049. Wanakah Member, Ludlowville Formation. Ledges along shore of Lake Erie, just south of mouth of Eighteen Mile Creek.</p> <p>3050. Windom Member, Moscow Formation. Exposure in cliff at shore of Lake Erie, about 0.5 mile south of loc. 3049.</p> <p>3051. Tichenor Member, Ludlowville Formation. Cazenovia Creek at Northrup Road, Erie County, New York.</p> <p>3052. Windom Member, Moscow Formation. Cazenovia Creek at Springbrook, New York, upstream from falls.</p> <p>3053. Arkona Formation. Same as UMMP loc. B.</p> <p>3054. Hungry Hollow Formation. Same as loc. 3053.</p> <p>3055. Hungry Hollow Formation. Same as UMMP loc. A.</p> <p>3056. Widder Formation. Same as loc. 3055.</p> <p>3057. Upper Ferron Point Formation. Same as UMMP loc. 38.</p> <p>3058. ?Genshaw Formation. Roadcut on Michigan Rt. 23, 10.6 miles south of junction of rts. 23 and 65.</p> <p>3059. Alpena Formation. Quarry of the Huron Portland Cement Company, Alpena, Michigan.</p> <p>3060. Gravel Point Formation. Same as UMMP loc. 14.</p> <p>3061. Four Mile Dam Formation. Exposures just below Four Mile Dam, south side of Thunder Bay River, west of Alpena, Michigan.</p> |
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3062. Thunderbay Formation. Same as UMMP loc. 35.
3063. Silica Formation. Same as UMMP loc. E.
3064. Mahantango Formation. Vicinity of Dingman's Falls, Pennsylvania.
3065. Lower Mahantango Formation. 0.2 mile south of loc. 3066, on Pennsylvania Rt. 191.
3066. "Centerfield" Member, Mahantango Formation. Exposure on Pennsylvania Rt. 191, about 4 miles north of Stroudsburg, Pennsylvania.
3067. "Centerfield" Member, Mahantango Formation. County road between Pennsylvania Rt. 209 and Saylorsburg, Pennsylvania, 2.0 miles south of Rt. 209.
3068. "Centerfield" Member, Mahantango Formation. Vicinity of Pohopoco Creek, in road cut on county road 2.5 miles east of Mahoning Valley exit of the Northeast extension of the Pennsylvania Turnpike. Near Forest Inn, Pennsylvania.
3069. ?"Centerfield" Member, Mahantango Formation. Exposure on north side of Pennsylvania Rt. 443, on western edge of Leighton, Pennsylvania.
3070. Upper shale Member, Mahantango Formation. Near Girty's Notch, near nose of Half Falls Mountain, in stream bed on west side of Susquehanna River, 6 miles north of intersection of Rt. 15 and U. S. Rt. 22 at Amity Hall, Pennsylvania.
3071. Upper shale Member, Mahantango Formation. Borrow pit along road, south flank of Mahanoy Ridge, east from Pennsylvania Rt. 34, south of New Bloomfield, Pennsylvania.
3072. Frame Member, upper Mahantango Formation. Roadcut along U. S. Rt. 22, opposite Huntingdon, Pennsylvania.
3073. Frame Member, upper Mahantango Formation. Roadcut on U. S. 220, 0.8 mile south of Newry, Pennsylvania.
3074. ?Upper Mahantango Formation. Behind State Police barracks in La Vale, Maryland, along U. S. Rt. 40.
3075. Upper Mahantango Formation. Railroad cut, just south of crossing of twenty-first Lane, off U. S. Rt. 220 in Maryland, 1 mile north of Keyser, West Virginia.
3076. Romney Formation. 0.5 mile north of junction of Rt. 50 and Rt. 28 in Romney, West Virginia, on Rt. 28 at junction with Central Avenue.
3077. Upper Romney Formation. Exposure on Rt. 50 opposite Methodist Children's Camp, on western edge of Burlington, West Virginia.
3078. Dundee limestone. Same as UMMP loc. E.
3079. Skaneateles Formation. Borrow pit on southern side of road along southern shore of Boone Reservoir, Madison County, New York.
- AMNH JAMES HALL AND G. K. GREENE COLLECTIONS
1. Milwaukee Formation. Same as UMMP loc. G.
 2. *Microcylus* zone of St. Laurent limestone. Exposure in east bank of Mississippi River at Devils Bakeoven, north of Grand Tower, Illinois.
 3. "Hamilton" (Cedar Valley), Rock Island, Illinois.
 4. Tully Formation. Penn Yan, New York.
 5. ?Widder Formation. Bosanquet, Ontario.
 6. Silver Creek Formation. G. K. Greene Collection. Near Watson, Clark County, Indiana.
 - 6A. Silver Creek Formation. G. K. Greene Collection. Near Charlestown, Clark County, Indiana.
 7. ?Windom Member, Moscow Formation. Moscow, New York.
 8. "Upper Helderberg" (almost certainly Dundee or Delaware Formations), possibly from "Kelly's Island," Ohio.
 9. Chemung. Chemung Creek, New York.
 10. Mahantango Formation (?upper). Top of hill, north side of Cumberland, Maryland.
 11. Romney Formation. Mouth of the Cacapon River, Virginia.
 12. Hamilton equivalent. Probably from Virginia.
- UNIVERSITY OF MICHIGAN MUSEUM OF PALEONTOLOGY,
ALL LOCALITIES FROM STUMM, 1953, EXCEPT THOSE IN
PARENTHESES
- A. Arkona, Hungry Hollow, and Widder Formations. Rock Glen on the Ausable River, 1 mile east and $\frac{3}{4}$ mile north of Arkona, Ontario.
 - B. Arkona, Hungry Hollow, and Widder Formations. Hungry Hollow on the Ausable River, 2 miles north and $\frac{3}{4}$ mile east of Arkona, Ontario.
 - C. Widder Formation. Brick and tile yard, $\frac{1}{2}$ mile north of Thedford, Ontario.
 - (I). Arkona Formation. Fraser Farm, about 3 miles northwest of Arkona, Ontario.
 - D. Plum Brook Formation. Ledges along tributary of Pipe Creek, $\frac{1}{4}$ mile east of Bloomingville, Ohio.
 - E. Silica Formation. (North) quarry of the Medusa Portland Cement Company at Silica, $1\frac{1}{2}$ miles southwest of Sylvania, Ohio.
 - F. Ten Mile Creek Formation. Ten Mile Creek, $\frac{1}{2}$ mile south of Silica, Ohio.
 - G. Milwaukee Formation. Milwaukee, Wisconsin.
 - 7B. Upper Petoskey Formation, *Schizophoria* bed. Limestone ledges along shore of Lake Michigan, from $1\frac{1}{10}$ – $1\frac{1}{2}$ miles north of Norwood, Michigan, near center of North line, sec. 26, T. 33 N, R. 9W.

14. Gravel Point Formation. Quarry of Petoskey Portland Cement Company (now Penn-Dixie Portland Cement Company), about $1\frac{1}{2}$ miles west of Petoskey, Michigan, SW $\frac{1}{2}$ sec. 2 and SE $\frac{1}{2}$ sec. 3, T. 34 N, R. 6W.
- 14e. Gravel Point Formation. Abandoned "Bell" Quarry and ledges on shore about 2 miles east of Bay Shore, Michigan, near NE corner sec. 8, T. 34 N, R. 6W.
- 15b. Gravel Point Formation. Shore of Little Traverse Bay from 9-Mile Point to 2.5 miles west, Charlevoix County, Michigan, T. 34 N, R. 7W.
21. Lower Petoskey Formation. Kegomic Quarry on south shore of Mud Lake just east of Harbor Springs Road (Mich. highway 131), about $\frac{1}{4}$ mile north of its termination on U.S. 31, 1 mile east of Bay View, Michigan, SE $\frac{1}{4}$ SW $\frac{1}{4}$ sec. 27, T. 35 N, R. 5W.
31. Bell Formation. Quarry of Michigan Limestone and Chemical Company at Calcite, Michigan, near Rogers City, 10 sections on SE part T. 35 N, R. 5E and adjacent townships.
35. Thunderbay Formation. Bluffs on northeast shore of Partridge Point, 4 miles south of Alpena, Michigan; extends from center into SE $\frac{1}{2}$ sec. 11, T. 30 N, R. 8E.
38. Ferron Point Formation. Abandoned quarry of Kelley's Island Lime and Transport Company, Rockport, Michigan, sec. 6, T. 32 N, R. 9E.
- (II). Alpena Formation. Quarry of the Huron Portland Cement Company, Alpena, Michigan.
- (III). Norway Point Formation. Shale bank on the south side of Thunder Bay River, about 1 mile below Four Mile Dam, west of Alpena, Michigan.
- (IV). Potter Farm Formation. Shale pit on Potter Farm just west of Evergreen Cemetery, western limits of Alpena, Michigan.
51. Upper Ferron Point and Genshaw Formations. Abandoned shale pit of Alpena Portland Cement Company, about 1 mile east and $\frac{1}{8}$ mile north of Genshaw School and 8 miles northeast of Alpena, Michigan, SE $\frac{1}{4}$ sec. 18, T. 32 N, R. 9E.
53. Alpena and Dock Street Formations. Abandoned quarry of the Thunderbay Limestone Company, eastern edge of Alpena, Michigan, SE $\frac{1}{4}$ sec. 14, T. 31 N, R. 8E.
114. Genshaw Formation. Ledges along Long Lake Road, near junction with Bell Road, south of Long Lake, Alpena County, Michigan, sec. 22, T. 32 N, R. 8E.

NATIONAL MUSEUM OF NATURAL HISTORY

1. Basal 18 inches, Rockport Quarry Limestone. Same as UMMP loc. 38.
- 1A. Ferron Point Formation. Same as UMMP loc. 38.
2. Upper Ferron Point Formation. Quarry of the Huron Portland Cement Company, Alpena, Michigan.
3. "Hamilton" (?Genshaw Formation). Ledges along Long Lake Road, north of Alpena, Michigan.
4. Upper Alpena Formation. Same as UMMP loc. III.
5. Thunderbay Formation. Same as UMMP loc. 35.
6. Lower Potter Farm Formation, big *Cranaena* zone. Shale pit at Alpena Cemetery, on west side of Alpena, Michigan.
7. Potter Farm Formation. Bank of Thunderbay River west of Alpena, Michigan.
8. Potter Farm Formation. 2 miles west of Alpena, Michigan.
9. Gravel Point Formation. Same as UMMP loc. 14.
10. Milwaukee Formation. Same as UMMP loc. G.
11. Upper Cedar Valley Formation. Banks of Mississippi River and quarries near Buffalo, Iowa.
12. Cedar Valley Formation, *independensis* zone. West edge of Solon, Iowa.
13. Ragland Formation. Ragland, St. Clair County, Alabama.
14. Stafford Formation. 2 miles north of Canada, New York.
- 14A. Stafford Formation. Stafford, New York.
- 14B. Stafford Formation. Le Roy, New York.
- 14C. Stafford Formation. Batavia, New York.
15. Pompey member, Skaneateles Formation. Pratt's Falls, Pompey, New York.
16. ?Skaneateles Formation. Morrisville, New York.
17. Skaneateles shale. Cayuga County, New York.
18. West Brook member, Tully Formation. Arab Hill Ravine, north end of Peruyter Reservoir, New York.
19. West Brook member, Tully Formation. Tinkers Falls, Truxton, New York.
20. Chemung. Spencer Lake Ravine, 2.5 miles north of Spencer, New York.
21. Mahantango Formation. Potts Grove, Pennsylvania.
22. ?Upper shale Member, Mahantango Formation. Same as AMNH loc. 3071.
23. Romney Formation. U.S. 52, 10 miles east of Berkeley Springs, West Virginia.
24. Romney Formation. West Virginia.
25. Romney Formation. Fort Valley, Virginia.

26. "Hamilton." Strasburg, Virginia.
 27. Delaware Formation. Columbus, Ohio.

STATE UNIVERSITY OF IOWA

Belanski collection, listed according to Belanski's station numbers, some of which have been identified by Harrell L. Strimple.

- 139-2. Probably Rapid Member, Cedar Valley Formation. Sanders Creek, north of Iowa City in Coralville Reservoir area.
 145- "Pholidostrophia zonule," Coralville Member, Cedar Valley Formation. Same as loc. 139-2.
 147-2. "triangulatus zonule." Probably Solon Member, Cedar Valley Formation. Locality unknown.
 168-3. "Gypidula comis zonule," Cedar Valley Formation. SW NW sec. 24, T81, Rt. 5.
 170-1. "Brandon substage, *Phacops rana* zonule," Cedar Valley Formation, NW NE sec. 26, T81, Rt. 5.
 183-5. "Brandon substage, *P. rana* zonule," Cedar Valley Formation. Locality unknown.
 190. "Brandon substage, *Streptasma* zonule," Cedar Valley Formation. Locality unknown.
 191-8. "Vinton substage, *Ptyctodus ferox* zonule," Cedar Valley Formation. Locality unknown.
 191-9. "Brandon substage, *Phacops rana* zonule," Cedar Valley Formation. Locality unknown.

- 191-13. "Brandon substage," Cedar Valley Formation. Locality unknown.
 191-16. "Brandon substage, *Euryocrinus zonule*," ?Rapid Member, Cedar Valley Formation, near Brandon, Iowa.
 ———. "Brandon substage," Cedar Valley Formation. Locality unknown.

UNIVERSITY OF IOWA NON-BELANSKI MATERIAL

1. Cedar Valley Formation. South side of Spillway, Lake McBride, Iowa.
2. Cedar Valley Formation. N $\frac{1}{2}$ NE $\frac{1}{4}$, sec. 26, T.81N, R.6W., Johnson County, Iowa.
3. Milwaukee Formation. Same as UMMP loc. G.
4. ?Solon Member, Cedar Valley Formation. Linn Junction, Iowa.
5. ?Solon Member, Cedar Valley Formation. Solon, Iowa.

NEW YORK STATE MUSEUM

1. Tully Formation. Ovid, New York.
2. Stafford Formation. Stafford, New York.
3. Hamilton Group. Seneca, New York.

MUSEUM OF COMPARATIVE ZOOLOGY, HARVARD UNIVERSITY

1. Silica Formation. Same as UMMP loc. E.

COLGATE UNIVERSITY

1. Silica Formation. Same as UMMP loc. E.

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