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LOWER MIDDLE DEVONIAN
SPECIES OF THE TRILOBITE
PHACOPS EMMRICH IN
NORTH AMERICA

NILES ELDREDGE

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ABSTRACT

SIX SPECIES (one new) including 20 subspecies (4 new) of *Phacops* are recognized from the Lower and Middle Devonian of North America. Gedinnian-Siegenian species include *P. logani* Hall, 1861, and *P. claviger* Haas, 1969. *Phacops clarksoni*, new species, occurs in the Emsian Schoharie Formation of New York, and *P. cristata* Hall, 1861, occurs in the Emsian and Eifelian of the Appalachian Province. *Phacops iowensis* Delo, 1935, and *P. rana* (Green, 1832) occur in Givetian strata.

A conservative position is taken on generic nomenclature and defended herein; all species, with the

exception of *P. rana* are closely related and belong to the same monophyletic taxon.

Special topics include a quantitative analysis of eye polymorphism and ontogeny in *Phacops logani birdsongensis* Delo, 1940, and *P. logani raymondi* (Delo, 1935), and of eye ontogeny in *Phacops cristata stummi*, new subspecies and *P. c. canadensis* (Stumm, 1954).

Cladistic methodology in paleontology is briefly discussed, and theories of relationship among all subspecies and species are presented. A key to all Devonian phacopid taxa considered valid herein is included.

INTRODUCTION

MANY SPECIES and "varieties" of the trilobite *Phacops* Emrich have been described from Devonian rocks in North America. Of these, all but one are associated with the Appalachian Faunal Province. The six species recognized as valid herein include *P. logani* Hall, 1861, from the Gedinnian and Siegenian of the Appalachian Province; *P. claviger* Haas, 1969, from the Siegenian of Nevada; *P. clarksoni*, new species, from the Emsian of the Appalachian Province; *P. cristata* Hall, 1861, from the Emsian and Eifelian of the Appalachian Province; and *P. rana* (Green, 1832) and *P. iowensis* Delo, 1935 from the Givetian of eastern and central North America. Evidence will be adduced in the present study showing that all species except *P. rana* are closely related. *Phacops iowensis* and *P. rana* have been discussed at length elsewhere (Eldredge, 1972b). Only *P. logani*, *P. clarksoni*, and *P. cristata* are described herein.

The following subspecies are recognized herein: *Phacops logani logani* Hall, 1861; *P. l. birdsongensis* Delo, 1940; *P. l. raymondi* (Delo, 1935); *P. l. clarkei*, new subspecies; and a new form, termed herein *P. l.* subspecies A. Seven subspecies are recognized for *P. cristata*: *P. c. cristata* Hall, 1861; *P. c. bombifrons* (Hall, 1861); *P. c. nasutus* (Stumm, 1954); *P. c. canadensis* (Stumm, 1954); *P. c. stummi*, new subspecies; *P. c. gaspensis* (Clarke, 1908), and *P. c. variabilis*, new subspecies. Valid subspecies of *P. rana* include *P. r. rana* (Green, 1832); *P. r. milleri* Stewart, 1927; *P. r. crassituberculata* Stumm, 1953; *P. r. norwoodensis* Stumm, 1953; and *P. r. paucituberculata* Eldredge, 1972. *Phacops iowensis iowensis* Delo, 1935, *P. i. southworthi* Stumm,

1953, and *P. i. alpenensis* (Stumm, 1953) also continue to be recognized herein.

Two familiar names have been synonymized. *Phacops cristata* var. *pipa* Hall and Clarke, 1888, is a junior synonym of *P. bombifrons* Hall, 1861 (considered *P. cristata bombifrons* herein). *Phacops hudsonicus* Hall, 1861, is considered the small-eyed variant of *P. l. logani*.

METHODOLOGY

Paleontological systematics is currently at a crossroads. Some of the ferment in theoretical methodology in systematics has begun to appear in the paleontological literature in recent years. Thus, authors such as Kaesler (1969) and Rowell (1969) would have paleontologists adopt the phenetic approach, basing their classifications and assessments of "affinity" on an overall resemblance model utilizing the various algorithms of numerical taxonomy. Others (e.g., Gaffney, 1972; Schaeffer, 1972; Eldredge, 1972a, 1972b; Schaeffer, Hecht, and Eldredge, 1972) have adopted, in whole or part, the theoretical stance of the "cladists" or "phylogenetic systematists" (e.g., Hennig, 1966; Brundin, 1968; Nelson, 1970). From this point of view, phylogeny is considered literally, and solely, as genealogy. Reconstructions of phylogenetic relationships become strictly a matter of recognition of nodal, or branching points, and are formulated by the identification of shared, derived characters. Degree of similarity or divergence is ignored; other phylogenetically oriented systematists have attacked this position,

holding that patristic, as well as cladistic, information is crucial to the entire phylogenetic picture of a group of organisms. It is perhaps no coincidence that at least some cladists (e.g., Eldredge, 1971b; Eldredge and Gould, 1972) have argued that speciation is far more important than lineal (phyletic) evolution in the modification as well as proliferation of taxa (species), and that, consequently, cladistic events subsume the notion of patristic affinity.

It is true that, to date, the vast majority of (invertebrate) paleontologists have exhibited a remarkable professional homeostasis, and have remained relatively unmoved by the uproar in systematics in recent years. Indeed, a well-known and esteemed paleontologist rose at a recent national meeting of the Paleontological Society to exhort his colleagues to eschew aimless soul-searching into problems Darwin solved long ago, and get to the business at hand. Were it not for the fact that much of our methodological kit, at least in systematics and phylogeny reconstruction, is permeated by a host of outmoded and inadequate formulations, I would agree. But sadly most paleontological investigations of phylogeny deal with the stratigraphic record as a self-revelatory, if imperfect, ledger of evolutionary events. Numericists and cladists alike, despite their wholly different (and irreconcilable) outlooks, have at least combined to force a more detailed consideration of morphology. And it is morphology, far more than stratigraphic and paleobiogeographic distribution, which most clearly bears the imprint of evolutionary history. The phylogenetic "signal" presented by morphology is the clearest, if interpreted in the proper fashion, and for this reason, formulations of phylogenetic relationships should be based wholly on a morphological argument.

Colless (1972) has argued that all judgments of affinity, be they among individuals or phyla, should be done in the same way. This point of view is basically followed herein. That is to say, the demonstration of cohesion, or integrity, of a sample from a single locality over a short stratigraphic interval is effected by recognition of shared character states, in most cases, if not in all, different from those in other such samples. The arguments are therefore basically the same in kind as those adduced in the matter of interspecific relationships, and the delineation of, and interrelationships among, the various subspecies

recognized herein. However, discrimination of taxa (not their interrelationships) at the specific and infraspecific levels is legitimately abetted by the generally accepted fact that taxa of these ranks are biologically discrete units with a reality (in nature, at least) not shared by taxa of higher rank. Such discrete taxa naturally have a definite and nonarbitrary distribution in space and time, and I can see no reason why stratigraphic and geographic distribution should not be brought to bear on their delineation. Paradoxically, the common practice in paleontology is to rely most heavily on stratigraphic position to recognize species only when such taxa are otherwise acknowledged (or supposed) to represent arbitrary divisions of a phyletic continuum. In the sense of discrete, "real" units in nature, local populations, subspecies, and species can be thought of as "basic taxa" (Jardine, 1969), and careful arguments based largely on morphology, but including spatiotemporal distribution, can be used to recognize them.

A large array of cephalic measurements (see Eldredge, 1972b, p. 62) were taken in the course of the present study. Some basic measurements descriptive of shape are included, but little statistical analysis is presented. Such analysis will be presented separately (Eldredge, ms. a) in conjunction with a general discussion of evolutionary trends. The curious dimorphism of the eye within some populations of *P. logani*, however, was subjected to a factor analysis. The data were normalized first by variables, then by cases; a rotated solution was not obtained. For further details of computational techniques, see Eldredge (1972b). The calculations were performed on a Wang 154 electronic calculator, using a program written by the author.

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ABBREVIATIONS

AMNH, American Museum of Natural History,
Department of Invertebrate Paleontology.
NYSM, New York State Museum
UM, Université de Montréal, Département de
Géologie
UMMP, University of Michigan, Museum of
Paleontology
USNM, National Museum of Natural History,
Smithsonian Institution
VU, Vanderbilt University, Department of
Geology
YPM, Peabody Museum, Yale University

PREVIOUS WORK ON LOWER AND LOWER MIDDLE DEVONIAN PHACOIDS

The first formal contributions to our knowledge of Lower and Lower Middle Devonian species of *Phacops* in North America were made by James Hall (1861a, 1861b, 1862). Hall (1861a) described *P. logani* from the "Lower Helderberg Group" of New York and *P. hudsonicus* from the "compact beds (?=Kalkberg Formation) of the shaly limestone," at Becraft Mountain, Hudson, New York. That same year

(1861b), Hall described *P. cristata* from the Schoharie Grit, and *P. bombifrons* from the "limestone of the Upper Helderberg Group" (=Onondaga Limestone) of New York.

Hall and Clarke (1888) placed *P. bombifrons* into synonymy with *P. cristata*, and described the "variety" *Phacops cristata* var. *pipa*, from the Onondaga Formation, as basically a small *P. cristata* with fewer eye lenses and no thoracic spines. Clarke (1900, 1908-1909) made further contributions to the study of Lower Devonian phacopids, concentrating his attention mainly on the "Oriskany" faunas of New York and Gaspé Peninsula. He referred all samples of *Phacops* from these units to *P. logani*, naming only one new "variety," *Phacops logani* var. *gaspensis* (1908) from the Grande Grève Formation of Gaspé.

The next substantial work on the systematics of Lower and Lower Middle Devonian phacopids in North America was that of Delo (1935a, 1935b, 1940). In addition to discussing all previously described taxa, Delo (1935b) recognized the new species *P. raymondi* from the Haragan Formation of Oklahoma, and (1940) *Phacops logani* var. *birdsongensis* from the Birdsong shale of Tennessee. Stumm (1954) discussed *Phacops* samples from various Eifelian formations in Indiana, Michigan, and Ontario. In addition to elevating *P. cristata* var. *pipa* to the rank of full species, *P. pipa*, Stumm (1954) named the new species *P. nasutus* from the Jeffersonville Formation, and *P. canadensis* from the "Onondaga" Formation at Port Colborne, Ontario. Subsequent work included a redescription of the excellently silicified *Phacops* specimens from the Jeffersonville Formation, at the Falls of the Ohio River in southern Indiana (Stumm, 1964), and the description of a new species, *P. claviger* Haas from the Siegenian of Nevada (Haas, 1969). Campbell (1967) briefly discussed the *Phacops* from the Haragan Formation, alluding to the possibility of referring *P. raymondi* and *P. logani* to a new genus closely related to *Anaspis* Campbell. Finally, Eldredge (1972b, p. 59) briefly discussed the possibility that *P. logani*, *P. hudsonicus*, *P. raymondi*, *P. claviger*, *P. cristata*, *P. cristata* var. *pipa*, and *P. iowensis* (from the Givetian of North America) belong to a single, monophyletic taxon. The scanty data briefly presented by me (1972b, p. 59) purporting to document an evolutionary trend in reduction in dorsoventral files among these species, has since

proved to be somewhat in error. However, the conclusion that these taxa, plus additional ones described herein, do in fact comprise a closely related group, remains a central contention of the present paper.

A NOTE ON GENERIC NAMES

The genus *Phacops* Emmerich, 1839 is one of the more familiar and entrenched names of the paleontological literature. Originally almost embracing what is now (Harrington et al. 1959) considered a suborder (see discussion in Delo, 1940), the name *Phacops* continues to be restricted. Campbell (1967, p. 33–35) presented a careful redescription and restriction of the genus, including of the species relevant to the present discussion only *P. iowensis*. Dr. Campbell has recently drawn my attention to the description of a new genus and two new subgenera of Phacopinæ by Maximova (1971). *Paciphacops* (*Paciphacops*) Maximova includes *inter alia* the *logani* group, and *Paciphacops* (*Viaphacops*) includes, *inter alia*, the *P. cristata* group. Despite the availability of these *nomina*, and the implication in Campbell (1967) that a new genus be named for *raymondi*, *hudsonicus*, and *logani*, I prefer, for the present, to retain a more conservative nomenclature and refer all such species to *Phacops*. The reason is simple: in spite of Campbell's (1967, p. 29) arguments for recognizing "horizontal" (in both a biostratigraphic and phylogenetic sense) taxa, what amounts to a "zonation" of generic names within the Phacopinæ automatically creates a hodge-podge of paraphyletic and polyphyletic taxa. For example, if my assessment of the affinity of *P. iowensis* is correct, it is more closely related to *P. logani* than to *P. rana*. Yet, *P. iowensis* and *P. rana* are similar in many details of morphology (Eldredge, 1972b) and each resembles the other more than either resembles *P. logani*. Campbell's restricted definition of *Phacops* would include *rana* and *iowensis* in that genus, but exclude *logani*. Thus, should my judgment of affinity be accepted (I discuss this extensively later in this report), *Phacops sensu* Campbell, 1967 will become a polyphyletic group in anyone's sense of the term except Simpson's (1961). There is no doubt that the genus needs revision, but if monophyletically arranged groups are the goal, then vertical, not horizontal, taxa (in the phylogenetic, not necessarily the biostratigraphic sense) will have to be recognized and named.

STRATIGRAPHY AND COLLECTIONS

In a previous paper I (Eldredge, 1972b) examined the geographic and stratigraphic patterns of variation of *Phacops rana* in detail. Such a study was possible given the wide distribution of Middle Devonian ("Hamilton") sediments over eastern and central North America. Gedinnian-Eifelian rocks, in contrast, are less well suited to such studies. Aside from the long outcrop belts of the central and southern Appalachians, the distributions of rocks of these ages are spotty; in addition, with a few noteworthy exceptions, *Phacops* constitutes a rather minor element in the brachiopod-bryozoan assemblages most commonly encountered, and the usual rock type—"limestones"—further impedes the ready assembly of good samples of well-preserved material.

The exceptions to these generalizations are important, however, as they afford standards scattered here and there in space and time with which other poorer samples may be compared. Thus, the Haragan Formation and Birdsong Shale have both yielded large quantities of well-preserved specimens of *Phacops*, and silicified specimens are also obtainable locally from the Kalkberg and New Scotland formations of New York. Large amounts of exquisitely preserved *Phacops* specimens from the "Red Clay Layer" within the Jeffersonville Formation (Stumm, 1964) are to be found in many collections in the United States. The Schoharie Formation, too, has yielded large quantities of internal and external molds of *P. cristata*. The Needmore shale, especially in Pennsylvania and Virginia, and the Ragland sandstone of Alabama have also produced useful faunas.

The Onondaga Formation (see Oliver, 1954, 1956), of New York and adjacent areas, poses a special problem. It is difficult to obtain well-preserved specimens in the field, and great reliance has been placed on museum collections in this study. The older collections, however, do not recognize the several members of the Onondaga Formation, so a detailed biostratigraphy of *P. cristata* and "*P. cristata* var. *pipa*" within this unit is not possible now. The arguments on the systematics of the Onondaga samples are therefore based wholly on morphology and comparison with known patterns of variation in samples from correlative units.

I shall not attempt to revise any stratigraphic nomenclature or age assignments of any rock

TABLE 1
DISTRIBUTION OF SUBSPECIES OF *Phacops logani*, *Phacops cristata*, AND *Phacops clarksoni*

Formation	Taxon or Taxa Present
	GASPÉ (FORILLON)
York River	? <i>P. cristata gaspensis</i>
Grande Grève	<i>P. cristata gaspensis</i>
Cap Bon Ami	<i>P. logani logani</i>
Roncelles	<i>P. logani logani</i>
	GASPÉ (PERCÉ)
Murailles	<i>P. logani clarkei</i>
Mont Joli	<i>P. logani ?logani</i>
	NEW YORK
Onondaga	<i>P. cristata bombifrons</i>
Schoharie	<i>P. cristata cristata</i> ; <i>P. clarksoni</i>
Esopus	<i>P. ?cristata</i> subsp.
Glenierie	<i>P. logani clarkei</i>
Upper Helderberg	<i>P. logani</i> subsp. A; <i>P. logani</i>
Group	? <i>logani</i>
Lower Helderberg	<i>P. logani logani</i>
Group	
	CENTRAL AND SOUTHERN APPALACHIANS
Ragland	<i>P. cristata variabilis</i>
Needmore	<i>P. cristata variabilis</i>
Oriskany	<i>P. ?logani</i> subsp.
Helderberg Group	<i>P. logani logani</i>
	WESTERN TENNESSEE
Birdsong	<i>P. logani birdsongensis</i>
Ross	<i>P. logani birdsongensis</i>
	OKLAHOMA
Haragan	<i>P. logani raymondi</i>
	SOUTHERN INDIANA
Jeffersonville	<i>P. cristata stummi</i> ; <i>P. cristata nasutus</i>
	OHIO
Columbus	<i>P. cristata stummi</i> ; <i>P. cristata bombifrons</i>
	MICHIGAN AND SOUTHERN ONTARIO
"Onondaga"	<i>P. cristata canadensis</i> ; <i>P. cristata bombifrons</i>
Bois Blanc	<i>P. cristata stummi</i>
Amherstburg	<i>P. cristata stummi</i>

units. The correlative scheme accepted here follows Boucot and Johnson (1967); as explained elsewhere (Eldredge, 1972b), studies of geographic and stratigraphic variation in fossils must utilize a biostratigraphic correlative framework independent of the particular organisms under study. The Appendix contains a complete locality list of the samples examined in the course of the present study.

KEY TO NORTH AMERICAN DEVONIAN SPECIES
AND SUBSPECIES OF *Phacops*

- Ornament consisting of laterally elongated tubercles on anterior margin of anterior glabellar lobe, lateral cephalic margins, occipital lobe, and axial lobes of thorax and pygidium. Pygidial pleura flat, with interpleural furrows absent, or developed weakly on anterior one or two pairs of pleura . . . *rana* 2
Ornament consisting of rounded tubercles not transversely elongated. Two or more pairs of interpleural furrows well developed on pygidium 6
- Eyes with 18 dorsoventral files 3
Eyes with 17 or fewer dorsoventral files 4
- Eyes with eight or nine lenses in central dorsoventral files; lenses protruding from sclera throughout most of visual surface . . . *rana milleri*
Eyes with six or fewer lenses per dorsoventral file; lenses flush with sclera throughout most of visual surface *rana crassituberculata*
- Eyes with 17 dorsoventral files; flattened elongated tubercles extending up frontal slope of glabella *rana rana*
Eyes with 15, 16, or 17 dorsoventral files . . . 5
- Eyes with 15 dorsoventral files only; elongated and flattened tubercles extending far up frontal slope of glabella . . . *rana paucituberculata*
Elongated, flattened tubercles only on extreme anterior edge of glabella . . . *rana norwoodensis*
- Glabella with tubercles covered with granules; anterior cephalic doublure and vincular furrow granulated; postocular ridge large, present on internal mold; glabellar furrow 1p generally distinct and intercalating ring present; thorax generally with nodes along axial furrows 7
Glabella tuberculated, without granules superimposed; cephalic doublure with granules anteromedially, becoming wavy ridges posterolaterally, or with wavy ridges over entire surface; postocular ridge reduced on internal mold; intercalating ring present or absent; thorax without nodes on axial furrow in external mold 12
- Cephalon with large genal and occipital spines; eye with 16 dorsoventral files; thorax with axial spines on alternating segments . . . *claviger*
Genal spines small or absent; no occipital or thoracic spines *logani* 8
- Genal spines present in large-eyed forms; eye usually large, exhibiting little intrapopulation variation, with 15, 17, 18, or (rarely) 19 dorsoventral files, with many lenses; or, eye with 15 dorsoventral files and few lenses (genal spine usually absent in these forms) 9
Genal spines generally absent in large-eyed

- forms; eyes variable and dimorphic; small-eyed group with 13–15 dorsoventral files and relatively few lenses; large-eyed group with 14–19 dorsoventral files 11
9. Large-eyed group with 17, 18, or 19 dorsoventral files; small-eyed group with 15 dorsoventral files, or unknown 10
- Large-eyed group with 15 dorsoventral files; intercalating ring closely associated with composite glabellar lobe . *logani* subspecies A
10. Glabellar granulation extremely minute; composite glabellar lobe relatively flat; intercalating ring present, but closely associated with composite glabellar lobe medially *logani clarkei*
- Glabellar granulation conspicuous; glabellar furrow 1p continuous and intercalating ring well developed *logani logani*
11. Large-eyed form with 14–18 dorsoventral files (\bar{X} approx. 16), with 67–111 lenses (\bar{X} approx. 89); small-eyed forms with 13–15 dorsoventral files (\bar{X} approx. 14) and 21–40 lenses (\bar{X} approx. 35) *logani raymondi*
- Large-eyed forms with 16–19 dorsoventral files (\bar{X} approx. 17), with 63–83 lenses (\bar{X} approx. 73); small-eyed forms with 14–15 dorsoventral files (\bar{X} approx. 14.5) and 33–55 lenses (\bar{X} approx. 40.5). (There is less distinction between the large-eyed and small-eyed forms of *P. logani birdsongensis* than in *P. logani raymondi*) *logani birdsongensis*
12. Eye with 17 dorsoventral files and 82–90 lenses; genal spines large; no occipital spine; intercalating ring present, or partially merged with composite glabellar lobe. Vincular furrow becomes shallow anteromedially . . *clarksoni*
- Eye with 11–16 dorsoventral files 13
13. Intercalating ring generally wholly merged with composite glabellar lobe; glabellar furrow 1p merged with occipital furrow distally, obsolescent over composite glabellar lobe medially; eye with 14 dorsoventral files or fewer, with rare exceptions 14
- Intercalating ring variably present or absent within a population; eye monomorphic, with either 13 or 14 dorsoventral files, or variable, with 14–16 dorsoventral files 19
14. Eye with 14 dorsoventral files; rare variants with 15 dorsoventral files 15
- Eye with 11–14 dorsoventral files (\bar{X} approx. 13) and with 17–48 lenses. Genal spines generally large, no occipital spine 17
15. Glabella relatively inflated, not inclined at high anterodorsal angle; intercalating ring sometimes present in small specimens 16
- Glabella flat, inclined at high angle antero-dorsally; intercalating ring wholly lost; axial nodes present on thorax or unknown; no occipital node or spine 18
16. Genal spines large; occipital spine generally present; thoracic axial spines invariably (?) present; eyes large, with 48–81 lenses (\bar{X} approx. 72); anterior cephalic doublure with terrace lines completely, or with granules anteromedially *cristata cristata*
- Genal spines large or small; no occipital spine observed; thoracic axial spines in some cases present, generally absent; eyes small, with 39–64 lenses (\bar{X} approx. 48); anterior cephalic doublure with granules medially *cristata bombifrons*
17. Glabella with faint traces of “rosette” pattern of small tubercles superimposed on larger tubercles; intercalating ring variably merged with composite glabellar lobe, or present. Eye with 28–48 lenses (\bar{X} approx. 40). Genal spines short or absent . . . *cristata gaspensis*
- Glabella steeply inclined anterodorsally; genal spines generally large; intercalating ring wholly merged with composite glabellar lobe; eye with 17–40 lenses (\bar{X} approx. 30) *cristata canadensis*
18. Glabella smoothly rounded anteriorly *cristata stummi*
- Glabella pointed anteromedially, distinctly pentagonal *cristata nasutus*
19. Eye with monomorphic pattern of 13 dorsoventral files; anterior cephalic doublure ornamented with transverse wavy ridges *iowensis* 20
- Eye either monomorphic with 14, or variable with 14–16 dorsoventral files . *cristata variabilis*
20. Glabellar furrow 1p deeply incised, invariably continuous medially; genal angle near ventral margin of cephalon, not recurved dorsally; pygidial pleural furrows moderately incised and pleura not strongly arched *iowensis alpenensis*
- Glabellar furrow 1p variably incised, occasionally obsolescent medially; genal angles recurved dorsally; pygidial pleural furrows deeply incised and pleura highly arched . 21
21. Exoskeleton large for species; tubercles large, conical, of several size classes; glabellar furrow 1p moderately deeply incised, continuous medially *iowensis southworthi*
- Glabellar furrow 1p variably incised, occasionally obsolescent medially *iowensis iowensis*

THE *PHACOPS LOGANI* COMPLEX

FIVE SUBSPECIES of *Phacops logani*, two of which are new, are recognized herein. The species and its subspecies are diagnosed immediately below. Aspects of ontogeny, and the relationships among the taxa are discussed in the following section. A more complete redescription of *P. raymondi* (= *P. logani raymondi* herein) is being prepared by K. S. W. Campbell.

Phacops logani Hall, 1861

Phacops logani HALL, 1861a, p. 353, pl. 73, figs. 15–25.

Phacops hudsonicus HALL, 1861a, p. 355, pl. 73, figs. 26–28.

Phacops logani: CLARKE, 1900, p. 21, pl. 1, figs. 1–5.

Phacops logani: CLARKE, 1908 (1908–1909), pp. 103, 108, pl. 10, figs. 1–4, 7–9.

[*non*] *Phacops logani* var. *gaspensis* CLARKE, 1908 (1908–1909), p. 119, pl. 10, figs. 5, 6, 10–16.

Phacops raymondi DELO, 1935b, p. 423, pl. 48, figs. 2, 3.

Phacops logani: DELO, 1940, p. 19, pl. 1, figs. 8, 9.

Phacops logani var. *birdsongensis* DELO, 1940, p. 19, pl. 1, figs. 13–15.

DIAGNOSIS: Cephalon with pronounced anterior arch, formed by slight to moderately steep anterodorsal slope of composite glabellar lobe when cephalon oriented with dorsal margin of both visual surfaces in same horizontal plane (“standard orientation”). Anterior margin of composite glabellar lobe vertical. Glabellar furrows 2p and 3p distinct on external surface. Glabellar furrow 1p distinct distally, more shallow, and in some obsolescent medially. Glabellar lobe 1p continuous (“intercalating ring”), curving anteriorly medially, but not merged with or incorporated into, composite glabellar lobe. Distal portion of glabellar lobe 1p commonly set off by shallow (exsagittal) furrow, and produced into distinct node. Occipital lobe generally with distinct median node or spinule. Genal nodes or spinules commonly present.

Fixigonal moiety of ocular platform (Eldredge, 1972b) generally pronounced, strongly convex posterior to visual surface forming distinct post-ocular ridge on internal and external molds, and ornamented, sharply set off from librigenal moiety by shallow depression marking course of posterior ramus of facial suture. Eye variable in size, but not reaching posterior border furrow.

Dorsal surface of cephalon, including inter-lensar sclera generally covered with small granules. Small granules covering larger tubercles resembling rosettes on glabella, occipital lobe, palpebral lobe, and palpebral area. Tuberculation on dorsal surface of cephalon never flattened or elongate transversely. Cephalic doublure, including vincular furrow, covered with small granules, somewhat elongate distally. Eight or nine distinct notches present in distal portion of vincular furrow, oriented in exsagittal plane, formed by grooves in both proximal and distal walls of vincular furrow. Vincular furrow commonly shallow, at times almost absent, anteriorly.

Hypostoma poorly known, essentially same as for *P. claviger* (Haas, 1969, p. 648, pl. 82, fig. 5a–c). Hypostoma short, with continuous marginal furrow deeply impressed, and elongate posterior projection essentially absent (in contrast to e.g., *P. rana*). Central body rather flat. Maculae conspicuous, in anterolateral area of central body. Entire surface of hypostoma ornamented with granules.

Visual surface polymorphic both in number of dorsoventral files and in number of lenses per dorsoventral file. Total number of lenses and number of dorsoventral files covary to some extent, producing two discrete modes (“large”- and “small”-eyed forms). Distribution of dimorphs approximating 50 percent of each in some subspecies (e.g., *birdsongensis*, *raymondi*) or almost 100 percent in large-eyed forms (*logani sensu stricto*, *clarkei*, subspecies A). Large-eyed forms with variable number of dorsoventral files, ranging from 14 to 19; however, each sample having strong mode of either 16 or 17 and relatively small dispersion. Range in total lens number observed 67–117, usually averaging about 90, except in *birdsongensis* (approx. 73).

Small-eyed forms with variable number of dorsoventral files, ranging from 14–16 (one specimen only). Most samples with about equal distribution of 14 and 15. Range in total lens number observed 33–55, but rarely exceeding 40.

Area under visual surface commonly produced into callus-like thickening in small-eyed forms. Visual surface kidney-shaped in outline, with dorsal margin of visual surface in small-eyed forms having distinct downward curve.

Thorax variably ornamented with small granules on axial ring, in some coalesced into rosettes as on cephalon. Pleuron, especially posterior ramus, typically heavily granulated. Distal nodes of axial ring, possibly homologous with those of intercalating ring, generally well developed, but in some cases obsolescent. Thoracic nodes set off by sinuous longitudinal furrow generally incomplete medially. Tips of pleura in larger specimens with V-shaped notches on posteroventral surface, producing "pleural hook" for articulation with notches in vincular furrow.

Pygidium with six to nine axial rings plus terminal piece; terminal piece set off distinctly from posterior pleural field, not reaching posterior pygidial margin. Five or six pleura present, usually with five pairs of interpleural furrows. Entire pygidium commonly covered with granulation.

TYPE: According to Delo (1940, p. 19), NYSM 13885/2 is the "holotype," but as none was originally designated by Hall (1861a), this specimen should be considered the lectotype as designated by Hall and Clarke (1888, pl. 8A, fig. 19).

Phacops logani logani Hall, 1861

Figure 1

Phacops logani HALL, 1861a, p. 353, pl. 73, figs. 15–25.

Phacops hudsonicus HALL, 1861a, p. 355, pl. 73, figs. 26–28.

Phacops logani: CLARKE, 1908 (1908–1909), p. 103.

Phacops logani: DELO, 1940, p. 19, pl. 1, figs. 8, 9.

DIAGNOSIS: Occipital node variably developed. Genal spine commonly present, in some cases absent. Genal spine absent on the two small-eyed forms available. Glabellar furrow 1p variably completely distinct or obsolescent medially. Nodes on distal portions of thoracic rings generally large and distinct.

Eyes showing only slight indication of dimorphism in available population samples. Almost all specimens of large-eyed form. Large-eyed form with 17, occasionally 18, dorsoventral files. Observed range of total lens number 81–117, average 94. Small-eyed forms (known only from two specimens) with 15 and 16 dorsoventral files; observed total lens number 46 and 48, respectively.

TYPE: As for species.

MATERIAL EXAMINED: Approximately 150

specimens from the Kalkberg and New Scotland formations of New York; 10 specimens from the Roncelles Formation of Quebec. One specimen from the Quay Rock Member of the Cap Bon Ami Formation of Gaspé, is also referred to *P. logani logani*. However, additional specimens may prove to be more closely related to *Phacops logani* subspecies A. See Appendix for locality list.

DISTRIBUTION: Lower Devonian (Gedinnian) (= "Lower Helderberg Group") of Appalachians, ?Missouri, Gaspé. See table 1.

Phacops logani birdsongensis Delo, 1940

Figure 2

Phacops logani var. *birdsongensis* DELO, 1940, p. 19, pl. 1, figs. 13–15.

DIAGNOSIS: Occipital node variably developed. Genal spine commonly absent. Glabellar furrow 1p variably completely distinct or obsolescent medially. Nodes on distal portion of thoracic axial rings variably developed, but generally clearly distinct.

Eye showing about 50 percent distribution of dimorphism in available sample. Large-eyed forms with 17 dorsoventral files with single known exception (19). Observed range of total lens number 63–83, average 73. Small-eyed forms with 14 or 15 dorsoventral files; observed range of total lens number 33–55, average 40.

TYPES: According to Delo (1940, p. 20), the holotype is a single specimen, YPM 15192. However, YPM 15192 consists of several specimens (including one *Reedops deckeri*). Delo actually figured two specimens; I designate YPM 15192a the holotype and YPM 15192b the paratype pygidium.

MATERIAL EXAMINED: Approximately 59 specimens from the collections of Vanderbilt and Yale universities, and the American Museum of Natural History, were available. See Appendix for localities.

DISTRIBUTION: Birdsong shale and Ross limestone, Tennessee.

REMARKS: As I mentioned (1972b, p. 59), a single specimen in the collection of the National Museum of Natural History (USNM 78923) from the "Linden Group" of Tennessee, has but 13 dorsoventral files and in this and all other respects is indistinguishable from *P. iowensis southworthi* from the Givetian Hungry Hollow Formation of Ontario. I have seen no other specimens in the field or in museum collections

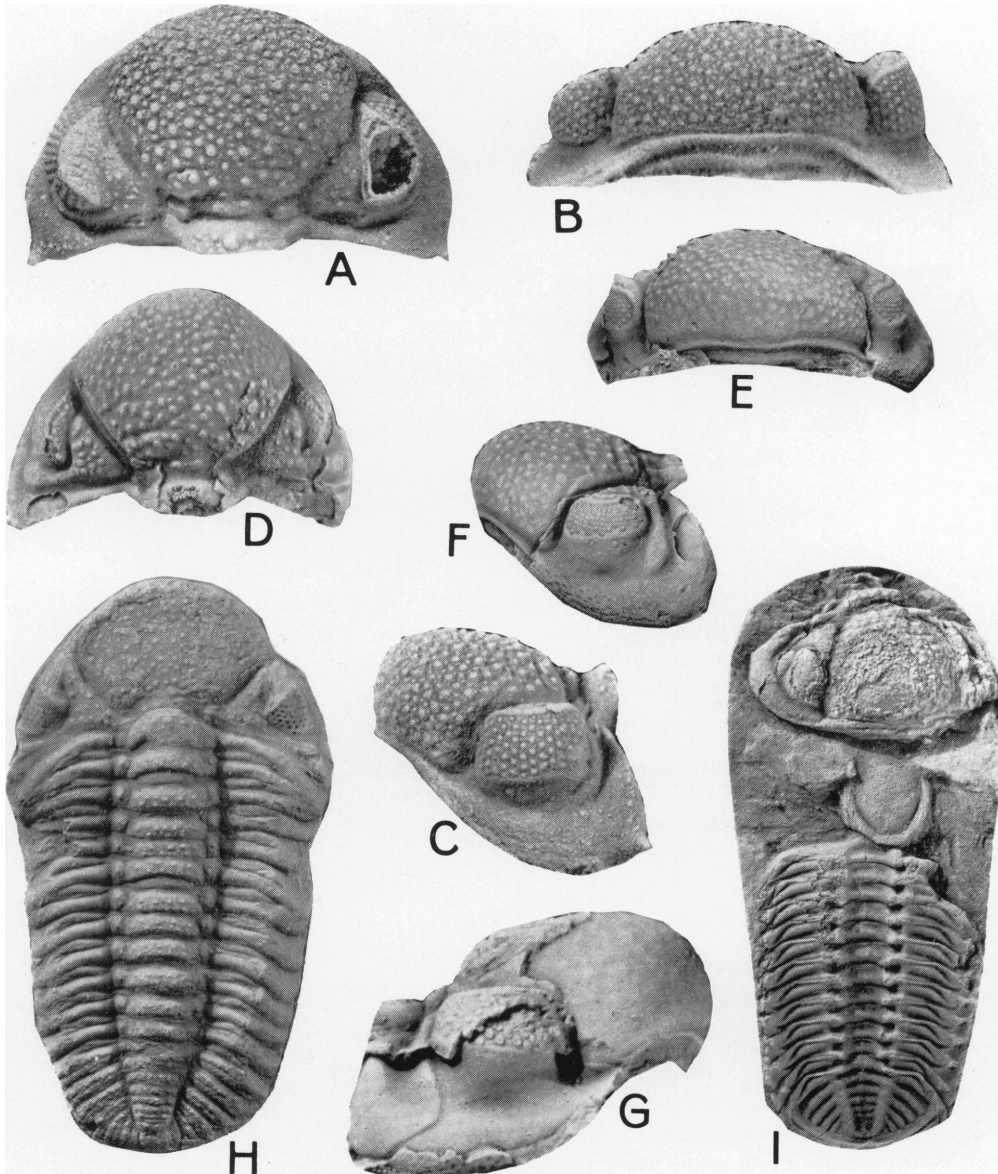


FIG. 1. *Phacops logani logani* Hall, 1861. A-C. Large-eyed form, NYSM 13885/3. New Scotland Formation near Schoharie, New York. $\times 4$. A. Dorsal view of cephalon. B. Frontal view. C. Left lateral view. D-F. Small-eyed form, AMNH 2613. Holotype of *P. hudsonicus* Hall. Kalkberg-New Scotland formations, Hudson, New York $\times 2$. D. Dorsal view. E. Frontal view. F. Left lateral view. G. Right lateral view of small-eyed form, AMNH 29249, Roncelles Formation. $\times 4$. H. Dorsal view of lectotype, NYSM 13885/2. $\times 1.5$. I. View of molt association with hypostoma, AMNH loc. 3091. $\times 1.5$.

from western Tennessee even remotely similar to this specimen, and conclude that it is best considered *P. iowensis southworthi* and that it comes (as its surrounding matrix suggests) from the Hungry Hollow Formation.

Phacops logani raymondi (DeLo, 1935)

Figure 3

Phacops hudsonicus: GIRTY, 1899, p. 571, pl. 61, fig. 4a-d.

Phacops raymondi DELO, 1935b, p. 423, pl. 48, figs. 2, 3.

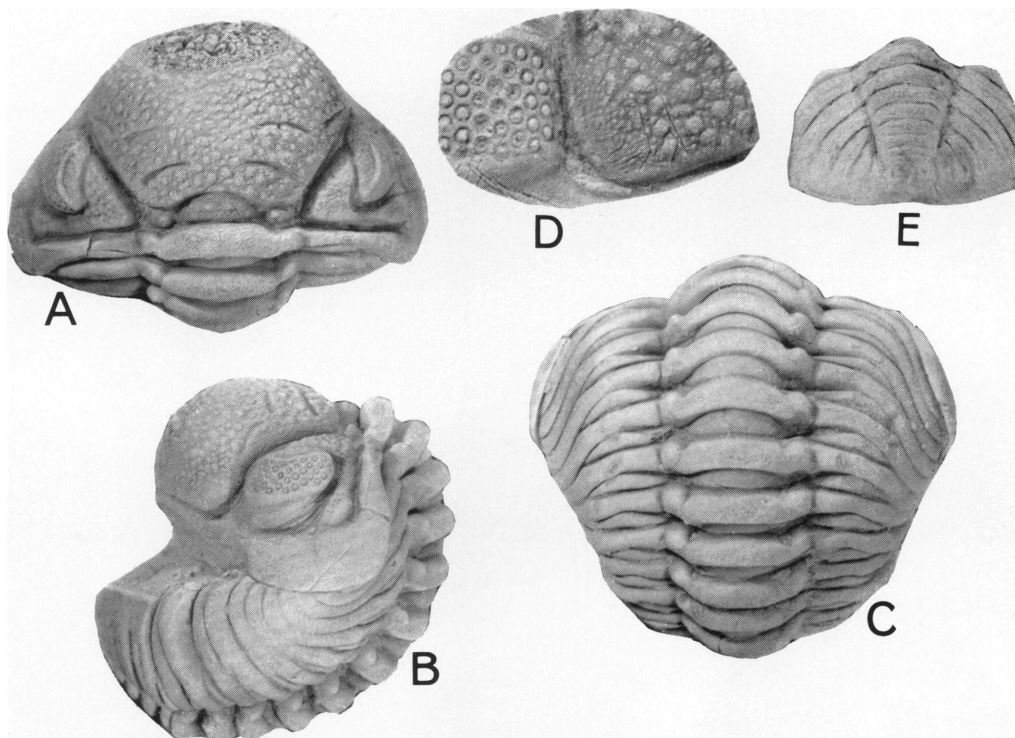


FIG. 2. *Phacops logani birdsongensis* Delo, 1940. Birdsong Formation, Tennessee. A–C. Holotype (small eyed form), YPM 15192A. $\times 2$. A. Dorsal view of cephalon. B. Left lateral view. C. Thorax. D. Right oblique view of cephalon of a large-eyed form, YPM 15192. $\times 5$. E. Paratype pygidium (of a small-eyed form), YPM 15192B. $\times 2$.

Phacops raymondi: DELO, 1940, p. 24, pl. 1, figs. 20, 21.

DIAGNOSIS: Occipital node variably developed. Genal spine absent or developed only as slight node. Glabellar furrow 1p variably completely distinct or obsolescent medially. Nodes on distal portions of thoracic axial rings variably developed, sometimes indistinct.

Eye showing about 50 percent distribution of dimorphism in available sample. Large-eyed forms ranging from 14–18 dorsoventral files, with strong mode of 16. Observed range of total lens number 67–111, average 89. Small-eyed forms with either 13, 14, or 15 dorsoventral files; observed range of total lens number 21–40, average 35.

TYPES: Holotype, University of Oklahoma A10, 304; paratype A10, 305. (Types not examined.)

MATERIAL EXAMINED: Approximately 70

specimens from the collections of the National Museum of Natural History, University of Michigan, and the American Museum of Natural History. See Appendix for localities.

DISTRIBUTION: Haragan Formation, Oklahoma.

REMARKS: A more complete discussion of the morphology, including aspects of dimorphism, of this taxon is under preparation by K. S. W. Campbell.

***Phacops logani clarkei*, new subspecies**

Figure 4

Phacops logani: CLARKE, 1900, p. 21, pl. 1, figs. 1–5.

Phacops logani: CLARKE, 1908 (1908–1909), p. 118, pl. 10, figs. 1–4, 7–9.

DIAGNOSIS: Glabella somewhat flatter than in other subspecies. Genal spines well developed.

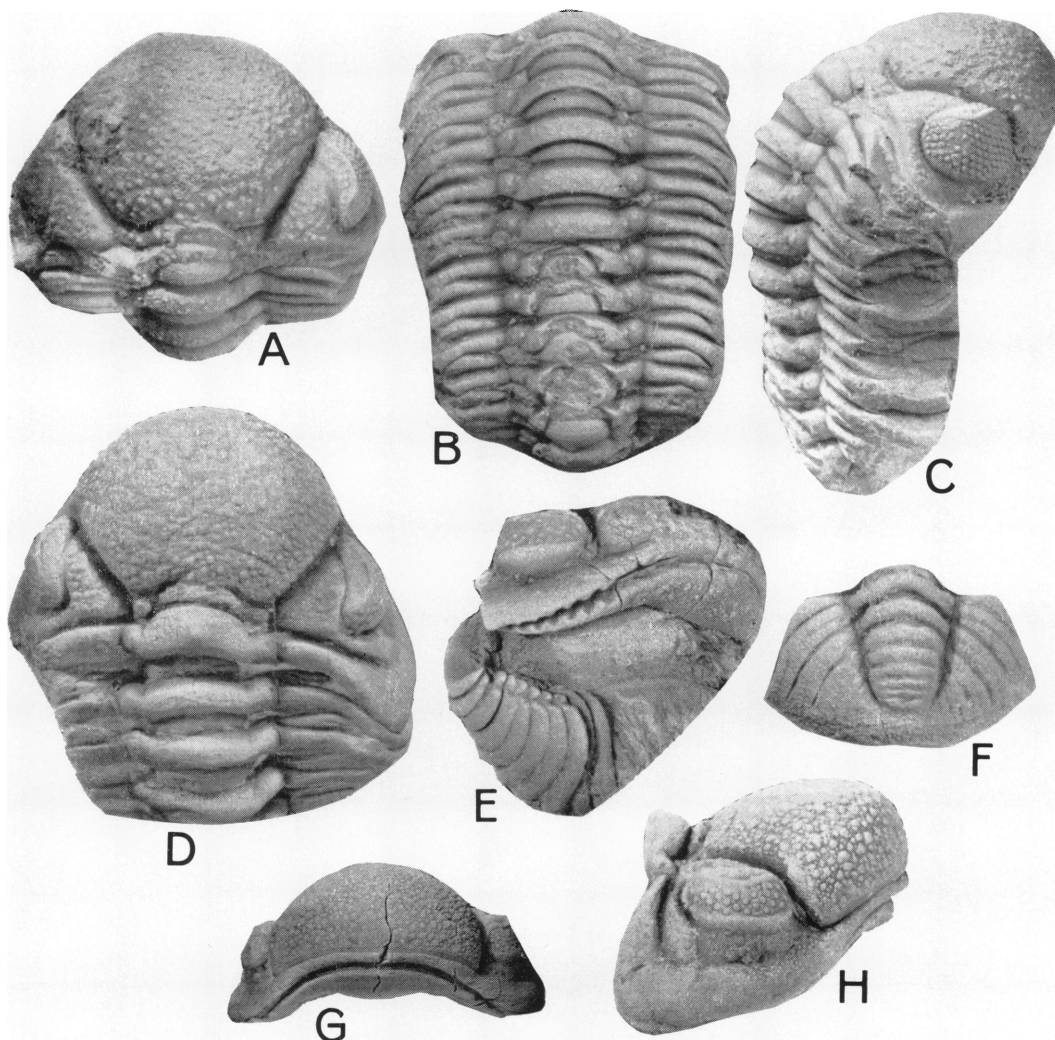


FIG. 3. *Phacops logani raymondi* (Delo, 1935). Haragan Formation, Oklahoma. A–C. Large-eyed form, USNM collection. $\times 3$. A. Dorsal view of cephalon. B. Thorax. C. Oblique right lateral view. D, F, H. Small-eyed form, USNM 34124. $\times 3$. D. Dorsal view of cephalon and anterior 3 thoracic segments. F. Pygidium. H. Right lateral view of cephalon. E. View showing distal notching and hooks on thoracic pleura, and notching of vincular furrow, USNM Acc. No. 173903. $\times 3$. G. Anterior view of cephalon of small-eyed form, USNM Acc. No. 174084. $\times 2$.

Glabellar furrow 1p generally indistinct medially, with some tendency toward incorporation of medial portion of intercalating ring into composite glabellar lobe. Fixigenal moiety of ocular platform relatively flat and less sharply distinct from librigenal moiety than in other subspecies. Postocular ridge reduced on internal mold. Nodes on distal portions of axial rings of thorax ranging from well developed in some

specimens (e.g., Murailles Formation sample) to indistinct in others (especially in Glenerie Formation, AMNH loc. 3094). Only large-eyed forms known; specimens from Murailles Formation with 17 dorsoventral files, and with about 86 lenses. Specimens from Glenerie Formation with 18 dorsoventral files and more than 100 lenses.

Ornamentation consisting of small tubercles

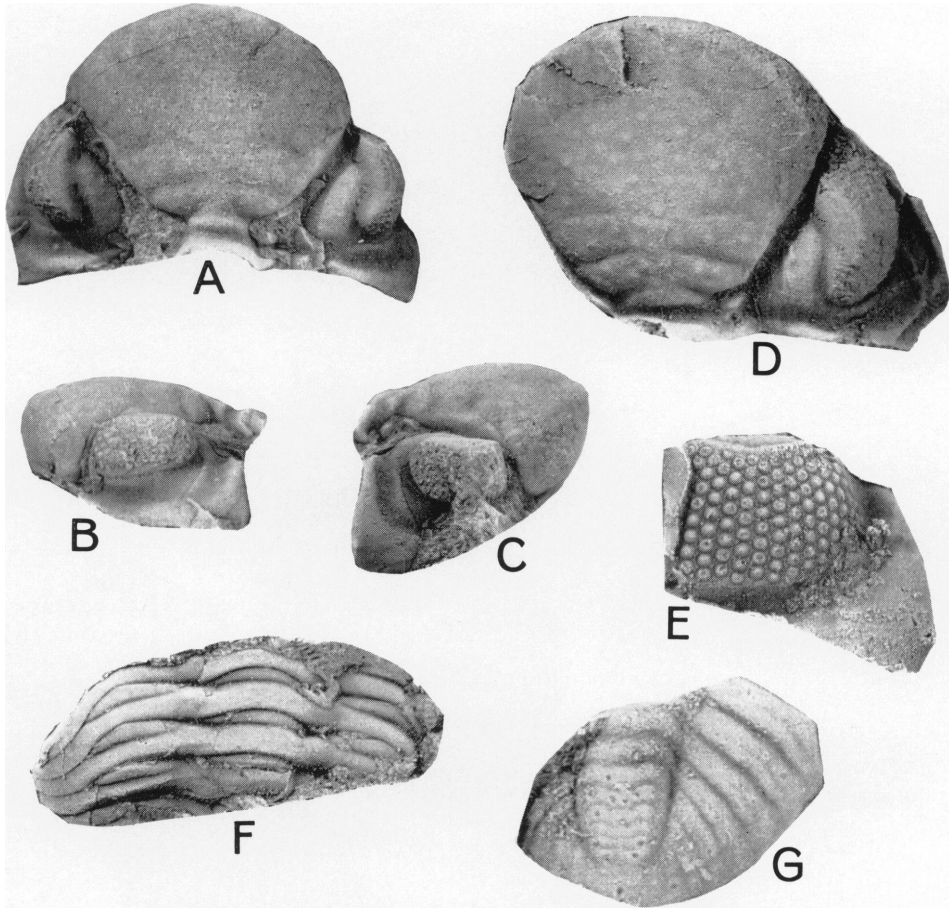


FIG. 4. *Phacops logani clarkei*, new subspecies. A-C. Holotype cephalon, AMNH 29240, AMNH loc. 3095. $\times 2$. A. Dorsal view. B. Left lateral view. C. Right lateral view. D. Dorsal view of paratype cephalon, AMNH 29241, AMNH loc. 3094. $\times 3$. E. Left eye, AMNH 29250, AMNH loc. 3094. $\times 4$. F. Thoracic segments, AMNH 29251, AMNH loc. 3094. $\times 2$. G. Paratype pygidium, AMNH 29242, AMNH loc. 3094. $\times 4$.

and groundmass of granulation much finer than in other subspecies, over cephalon, thorax, and pygidium.

TYPES: Holotype cephalon AMNH 29240 from the Murailles Formation. Paratype cephalon from the Glenerie Formation, AMNH 29241. Paratype pygidium AMNH 29242 from the Glenerie Formation.

MATERIAL EXAMINED: Approximately 78 specimens in the collections of the American Museum of Natural History. See Appendix for localities.

DISTRIBUTION: Murailles Formation at Percé, Gaspé Peninsula, Quebec; Glenerie Formation, Becraft Mountain, New York.

ETYMOLOGY: This subspecies is named for John M. Clarke, avid student of Oriskany fossils and one of the most outstanding paleontologists of any era.

REMARKS: *Phacops logani clarkei* is based on samples from two localities of Upper Siegenian ("Oriskany") age, which are separated by a considerable geographic distance. The two samples share the derived characters of a flattened postocular ridge, a tendency to incorporate the intercalating ring into the composite glabellar lobe, and a minute granulation over the dorsal surface of the exoskeleton. However, several consistent differences are noted between the two samples, which may

eventually warrant recognition of another subspecies to embrace the Glenerie specimens. The specimens from the Murailles Formation retain the thoracic axial nodes and the more typical lens arrangement of *P. logani logani*, whereas the specimens from New York appear advanced in reducing the former and having more lenses arranged, insofar as known, in 18 rather than 17 dorsoventral files.

Phacops logani subspecies A
Figure 5

DIAGNOSIS: Composite glabellar lobe less tumid and inclined anteriorly at lower angle than in *P. logani logani*. Intercalating ring reduced, partially incorporated into composite glabellar lobe.

Eye with 15 dorsoventral files, and total lens number of 73 in the only specimen known.

Hypostoma, thorax, and pygidium unknown.

REFERRED SPECIMEN: One cephalon, AMNH 29243.

DISTRIBUTION: Presumably Becraft Formation, New York.

REMARKS: This subspecies is recognized with some hesitation on the basis of a single cephalon. The morphology of the eye is quite distinct from all other *P. logani* known to me, with the sole exception of one specimen of *P. logani raymondi*.

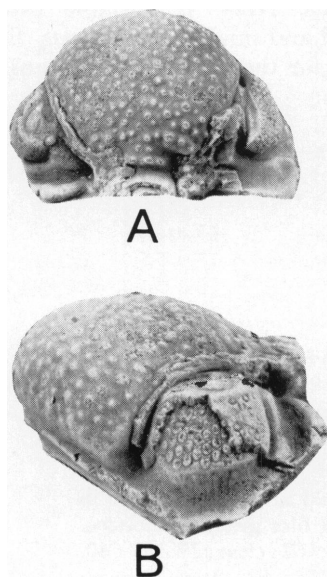


FIG. 5. *Phacops logani* subspecies A. Becraft Formation, Schoharie region, New York, AMNH 29243. A. Dorsal view. $\times 2$. B. Left lateral view. $\times 3$.

In addition, the character of the intercalating ring is sufficiently distinctive to warrant provisional subspecific status.

“BASIC TAXA” AND *PHACOPS LOGANI*

The existence of two, and perhaps three, eye variants of *P. logani* in both the Haragan and Birdsong formations, and, to a lesser extent, in some Lower Devonian units of the central and northern Appalachians, presents a difficult problem in geographic variation and intra-population genetics. Although Campbell (personal commun.) has been able to add other morphological features whereby the two eye variants may be distinguished in the Haragan fauna, there can be no doubt that all *Phacops* from the Haragan (as well as the Birdsong and other Appalachian faunas) possess a number of shared, derived characters that (1) show all specimens within any one formation to be closely related and (2) indicate that all are to be considered closely related to, if not actually conspecific with, *Phacops logani*. These characters are set forth in the diagnosis of *P. logani* above. Furthermore, such data pertaining to within-formation distribution of these trilobites indicate that while some units may produce different ratios of small-eyed versus large-eyed forms, the two are often found within the same small stratigraphic unit. I am reluctant, therefore, to recognize two subspecies of *P. logani* with such apparently insignificant differences in stratigraphic occurrence, and assume instead that each fauna presents a population of *P. logani* exhibiting its own peculiar distribution of eye polymorphism. If separate names are desirable, however, *Phacops hudsonicus* Hall, 1861 is available for the small-eyed form. Indeed, Girty (1899, p. 571) applied this name to the small-eyed variant in the Haragan fauna, while Delo (1935b) established the new species *P. raymondi* to embrace the large-eyed forms. Delo (1940) later reviewed all Lower Devonian species of *Phacops* in North America, and concluded that the two eye forms are recognizable, but intergrade, in the *Phacops* from the Birdsong shale, although he continued to recognize two distinct species in the Haragan.

The problem is further compounded by the rare occurrence of the small-eyed form in the central and northern Appalachians (i.e., Virginia-Gaspé Peninsula). Hall's type of *Phacops*

hudsonicus is based on a single cephalon from the "compact shaly beds at Becraft Mountain" (Hall, 1861a) (probably New Scotland or Kalkberg formations in modern usage). I have since seen this eye type in a single specimen each from the Roncelles Formation ("St. Alban Formation") and the Cap Bon Ami Formation (Quay Rock Member) from Gaspé. However, K. S. W. Campbell (personal commun.) informs me that he has seen additional specimens of the small-eyed variant from the "Indian Ladder" section (YPM 6954) now within John Boyd Thacher State Park in New York. Thus, the problem of "basic taxa" is definitely not unambiguous, but I prefer to interpret all occurrences of *Phacops* in the Lower Devonian Appalachian fauna as that of a single species, *Phacops logani*, among which five subspecies may be distinguished, not on the criterion of large-eyed versus small-eyed, but on various morphological criteria (including the precise nature of the eye polymorphism), as well as geographic, and to a lesser extent, stratigraphic distributions. The relationships among these subspecies are discussed following an examination of the nature of the eye polymorphism.

EYE POLYMORPHISM IN *PHACOPS LOGANI*

Eye polymorphism in *P. logani* was investigated quantitatively for two purposes: (1) to elucidate patterns of development, including

relationships among variables, and variability within a sample; and (2) to evaluate the degree to which these patterns are held in common among all *P. logani* available. For these purposes, three samples were delineated: (1) All Haragan *P. logani* (mixed localities); (2) All Birdsong *Phacops logani* (mixed localities, although almost all specimens are from the "trilobite zone" [Dunbar, 1919] at the northern end of the outcrop belt of the Birdsong Formation); and (3) all central and northern Appalachian *P. logani* mixed. It is obvious that only the Haragan and Birdsong samples are to be taken seriously from the point of view of intra-population developmental patterns. Indeed, even these two samples present serious difficulties, as the ideal situation of deriving a sample from a single bedding plane at one locality is far from achieved. However, degree of similarity in eye morphology can be effectively evaluated by considering mixed samples simultaneously.

Figure 6 gives a histogram for each sample showing frequency of number of dorsoventral files. In addition, two classes based on total lens number are indicated by crosshatching. In a previous study (1972b), I found that the intra-population variability in number of dorsoventral files (NDV) in *Phacops rana* and *P. iowensis* was effectively nil. In sharp contrast, although strong modes appear in *P. logani* populations, NDV is variable even among large-eyed and small-eyed variants (fig. 6). The raw data for these plots, plus means, standard

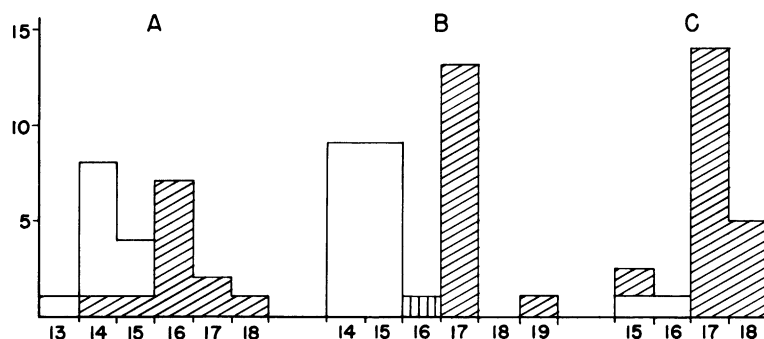


FIG. 6. Histogram showing frequency of large and small-eyed groups in samples of *Phacops logani*. Number of dorsoventral files given on bottom. A. *P. logani raymondi*; N=25; crosshatching: NLNS > 67; clear: NLNS < 40. B. *P. l. birdsongensis*; N=33; crosshatching: NLNS > 68; vertical lines: intermediate; clear: NLNS < 55. C. Combined *P. logani* from the central and northern Appalachians; N=22; crosshatching: NLNS > 70; clear: NLNS < 50.

TABLE 2

RAW DATA AND SUMMARY STATISTICS FOR THE PLOTS AND ANALYSES OF *Phacops logani birdsongensis*, *Phacops logani raymondi*, AND MIXED SAMPLES OF *Phacops logani* FROM THE CENTRAL AND NORTHERN APPALACHIANS.

(In micrometer units, where 6 units = 1 mm.)

Specimen	CL	NDV	NLNS
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<i>Phacops logani birdsongensis</i> (LARGE-EYED FORMS)			
1	58	17	70
2	78	17	71
3	86	17	75
4	80	17	76
5	82	17	73
6	68	17	73
7	74	17	74
8	78	17	74
9	83	17	68
10	63	17	73
11	75	19	83
\bar{X}	75.0	17.18	73.64
S_x	8.72	0.60	3.85
V	11.6	3.5	5.2

<i>Phacops logani birdsongensis</i> (SMALL-EYED FORMS)			
1	83	15	55
2	69	15	41
3	65	14	36
4	96	15	45
5	56	14	36
6	57	14	38
7	44	14	39
8	34	14	33
9	49	14	36
10	70	14	34
11	80	15	49
12	66	14	36
13	57	15	39
14	47	15	43
\bar{X}	62.36	14.43	40.0
S_x	16.75	0.51	6.18
V	26.9	3.6	15.4

<i>Phacops logani raymondi</i> (LARGE-EYED FORMS)			
1	69	16	91
2	63	16	86
3	71	16	95
4	72	16	100
5	66	17	97
6	66	18	111
7	63	16	83
8	57	16	84
9	53	14	73
10	81	17	67

TABLE 2—(Continued)

Specimen	CL	NDV	NLNS
11	60	16	94
12	70	15	87
\bar{X}	65.92	16.08	89.0
S_x	7.48	0.99	11.86
V	11.34	6.2	13.3

<i>Phacops logani raymondi</i> (SMALL-EYED FORMS)			
1	68	14	37
2	46	14	36
3	61	14	35
4	61	14	34
5	65	14	34
6	52	15	39
7	65	15	36
8	56	15	40
9	73	14	35
10	45	15	39
11	44	14	34
12	19	13	21
\bar{X}	54.58	14.25	35.0
S_x	14.68	0.62	4.88
V	26.9	4.4	13.9

<i>Phacops logani</i> , MIXED SAMPLES (LARGE-EYED FORMS)			
1	46	18	97
2	60	17	88
3	85	17	98
4	86	17	99
5	88	17	100
6	84	18	87
7	47	17	84
8	67	17	95
9	36	17	81
10	77	15	73
11	61	17	87
12	66	17	89
13	65	17	117
14	56	17	84
15	80	18	115
\bar{X}	66.93	17.07	92.93
S_x	16.25	0.70	11.98
V	24.3	4.1	12.9

<i>Phacops logani</i> , MIXED SAMPLES (SMALL-EYED FORMS)			
1	81	15	46
2	68	16	48
\bar{X}	74.5	15.5	47.0
S_x	9.19	0.71	1.41
V	12.3	4.56	3.0

Abbreviations: CL, cephalic length; NDV, number of dorsoventral files; NLNS, total number of lenses; \bar{X} , mean; S_x , standard deviation; V, coefficient of variation.

deviations, and coefficients of variation, are included in table 2. The taxonomic implications of this variability are considered below.

Total lens number (NLNS) was taken as a second variable, as, together with NDV, it serves to delineate the eye variants sufficiently clearly. An alternate approach would be to consider the number of lenses within each dorso-ventral file as a separate variable, but the patterns are clearer when the simple gross total is taken. Finally, total cephalic length (CL) was included as a rough measure of ontogenetic stage. I have not performed a "morphological integration" study similar to that in Eldredge (1972b, p. 67) but I assume instead that all major cephalic dimensions are isometric with respect to CL and thus of little added interest to the present problem.

The ontogeny of the phacopid eye is still poorly understood. However, the patterns of interaction of the three variables discussed below actually may serve to complicate, rather than elucidate, the major elements of the process. From these data, as well as much additional data (on *Phacops rana*; Eldredge ms. b), it is clear that, as holaspid ontogeny proceeds, lenses are added rapidly to the lower margin of the visual surface. Height and length of the visual surface increases more or less isometrically with total head size throughout ontogeny. At some point, the rate of lens addition slows down and in some instances may even become negative (Eldredge, ms. b); indeed, it is not unusual to find the largest values of NLNS in eyes of specimens considerably smaller than the largest observed. This phenomenon is found even within otherwise monomorphic groups (e.g., *P. rana milleri* Stewart).

Similarly, NDV is either invariant, slightly variable, or shows only moderate increase early in holaspid ontogeny. In the discussion that follows then, it should be kept in mind that the data are normalized both by rows and by columns, and the among-specimen variation seen, e.g., in proportion of NDV to CL, reflects the proportionate contribution of each variable to the composition of any one specimen. Thus, it is possible to have a linear array apparently showing variation in NDV within a population where NDV is in fact constant.

In any three-variable system, the square of row normalized data can be plotted on a ternary diagram (figs. 7-9). These data were

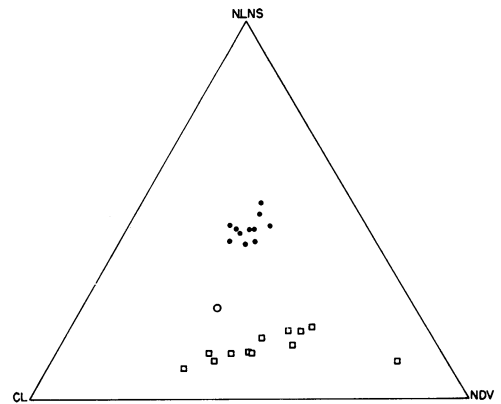


FIG. 7. Ternary diagram of squared normalized data for *Phacops logani raymondi*.

Symbols: ●, Large-eyed forms; □, small-eyed forms; ○, intermediate. For further explanation, see text.

column-normalized first, primarily so that NDV could contribute to the dispersion as clearly as do CL and NLNS. These plots are themselves interesting, although a factor analysis was necessary to recover the full structure of the data. The plot for *P. logani raymondi* (fig. 7) shows two major clusters. The upper cluster (the large-eyed forms) shows a homogeneous scatter, well differentiated from the lower, linear array (reflecting ontogeny) of small-eyed forms. There is one intermediate specimen, and one extremely small specimen not clearly aligned with either major group.

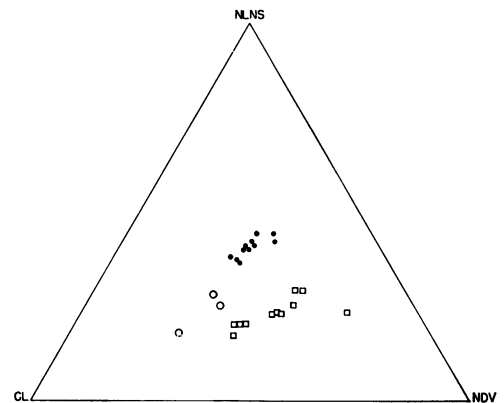


FIG. 8. Ternary diagram of squared normalized data for *Phacops logani birdsongensis*.

Symbols: ●, large-eyed forms; □, small-eyed forms; ○, intermediates. For further explanation, see text.

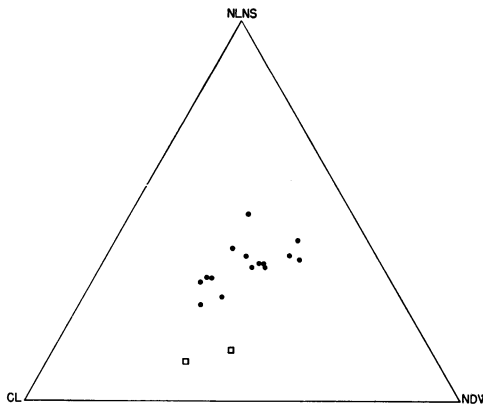


FIG. 9. Ternary diagram of squared normalized data for central and northern Appalachian mixed samples of *Phacops logani*.

Symbols: ●, large-eyed forms; □, small-eyed forms. For further explanation, see text.

Figure 8 shows a comparable plot of *P. logani birdsongensis*. Here, large-eyed forms do tend to exhibit a linear pattern reflecting ontogeny, as do the small-eyed forms. The two major clusters are somewhat closer to each other than they were in the *P. logani raymondi* plot (fig. 7). There are three intermediates shown, and again, a small specimen is present, not clearly associated with either of the other groups. Figure 9 shows a plot of all central and northern Appalachian specimens available to me. The major, linear cluster, somewhat rough as the sample is so heterogeneous, again reflects ontogeny. Two specimens, including the holotype of *P. hudsonicus*, form the lower cluster corresponding to the small-eyed forms.

These plots of normalized data are best understood after the data are subjected to a factor analysis. The data factored are the same as those plotted on the ternary diagram, with

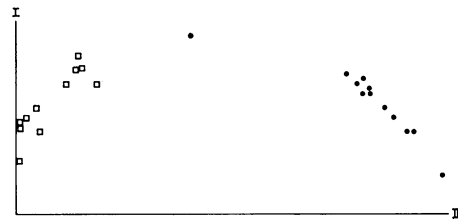


FIG. 10. Factor analysis plot for *P. logani raymondi*. Unrotated factors I and II.

Symbols: □, small-eyed forms; ●, large-eyed forms.

the exception that the normalized row data were not squared. Factor components for separate runs of *P. logani raymondi*, *P. logani birdsongensis*, and for all *P. logani* taken together, are given in table 3. The three analyses yielded closely similar results. I will consider the separate analyses of *raymondi* and *birdsongensis* first, as they are more likely a priori to yield coherent and meaningful results from an ontogenetic standpoint.

The results are best understood by plotting the factor coefficients (specimen scores) against two factors, yielding three plots for each analysis. Figures 10 and 11 show plots of factor I versus factor II for *raymondi* and *birdsongensis*, respectively. Both yield a fairly tight parabolic distribution; factor I in both instances can be considered a "maximization" plot, i.e., a high score on this factor indicates a maximum "balance" of values of all three parameters (CL, NDV, NLNS). Lower scores indicate a disruption of this balance, best explained by reference to one of the other two factors. Note that factor I is insufficient to separate the two eye groups, but that factor II clearly does so. In both analyses, a high score on factor II indicates a relatively high proportion of NLNS in relation both to CL and NDV (for *raymondi*) or

TABLE 3
FACTOR COMPONENTS FOR THREE FACTOR ANALYSES OF *Phacops logani*

	<i>P. logani raymondi</i> N=24			<i>P. logani birdsongensis</i> N=25			All <i>P. logani</i> N=75		
	I	II	III	I	II	III	I	II	III
CL	0.59	-.30	0.75	0.58	-.57	-.58	0.59	-.52	-.62
NDV	0.62	-.43	-.66	0.60	-.18	0.78	0.61	-.22	0.76
NLNS	0.52	0.85	-.07	0.55	0.80	-.24	0.54	0.83	-.18

For abbreviations, see table 2.

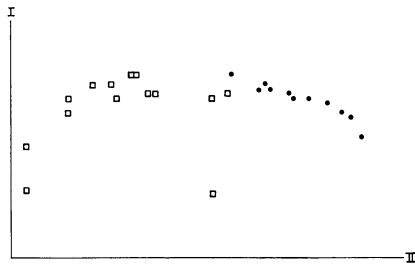


FIG. 11. Factor analysis plot for *P. logani birdsongensis*. Unrotated factors I and II.

Symbols: □, small-eyed forms; ●, large-eyed forms.

especially CL (*birdsongensis*). A low score indicates a disproportionately low number of lenses with respect to the other two variables.

The parabolic nature of figures 10 and 11 is thus easily interpreted. Large-eyed forms depart from the maximization of factor I by disproportionately increasing the number of lenses in relation to CL and NDV, whereas the small-eyed forms depart from maximization by decreasing NLNS. But upon closer examination of the plots, it is apparent that this variation in *birdsongensis* within both eye morphs is systematically controlled by ontogeny, i.e., there is close agreement between CL and the score of each specimen on factor II. The large-eyed *P. logani birdsongensis* increase maximization of factor I as ontogeny proceeds, by reducing the disproportionately large contribution of NLNS (factor II). At the same time, the small-eyed forms also show progressively decreasing scores along factor II during ontogeny, but reach a maximum value (factor I) early in ontogeny, and proceed to depart from the maximum by continued decreasing of NLNS in relation to the other two variables. In simple terms, rate of lens addition slows considerably in both groups during ontogeny; whether or not this rate drops to zero, or becomes negative (implying resorption) cannot be determined from the analysis.

The internal structure of the *raymondi* plot (fig. 10) is somewhat different. The large-eyed forms also show a negative relationship between factors I and II, implying that mutual maximization of the three variables (factor I) is disrupted by a disproportionately large number of lenses. However, here the largest specimens fall in the middle of the plot. Rather than reflecting ontogeny, we merely see intra-population variability. The internal structure of the small-

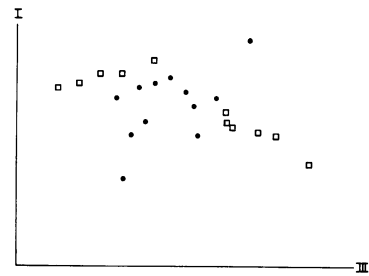


FIG. 12. Factor analysis plot for *P. logani raymondi*. Unrotated factors I and III.

Symbols: □, small-eyed forms; ●, large-eyed forms.

eyed form cluster is harder to interpret. As in the small-eyed *birdsongensis* cluster, there is an approach to maximization of factor I early in ontogeny, but by increasing lenses in proportion to CL and NDV. A second cluster shows a reverse trend, where factor I is minimized by decreasing the relative importance of NLNS. In sum, although plots of factor I versus factor II show similar patterns for the two population samples, their internal structure is somewhat different, and the ontogenetic process seems simpler, or at least more readily interpretable, for *birdsongensis* than for *raymondi*.

Although the components of factor III are signed differently in these two analyses, their interpretation is the same, i.e., there is an antagonistic relation between CL and NDV. For *P. logani raymondi* (fig. 12), a high score on factor III implies a proportionally small number of dorsoventral files with respect to CL, whereas for *P. logani birdsongensis*, the reverse is true. Both plots (figs. 12, 13) for large-eyed forms, show a fair alignment with ontogeny (size; CL here). However, for *birdsongensis* (fig. 13), maximization along factor I occurs throughout ontogeny by decreasing NDV in relation to

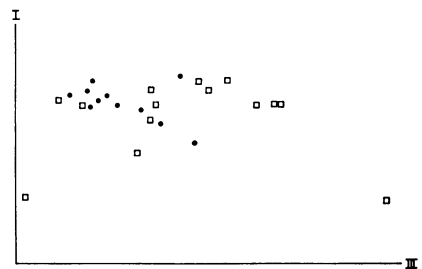


FIG. 13. Factor analysis plot for *P. logani birdsongensis*. Unrotated factors I and III.

Symbols: □, small-eyed forms; ●, large-eyed forms.

CL. Again, this obviously does not mean that dorsoventral files are actually being lost; rather, NDV is stabilized as CL increases. Although this is true of all populations of phacopid trilobites known to me, in large-eyed *P. logani birdsongensis*, the effect is to bring the three variables into better "balance" ("maximized") as holaspid ontogeny progresses. The reverse seems to be true of *P. logani raymondi*; although the correspondence of the plot of the large-eyed forms is perhaps less close with ontogeny, decrease in the ratio of NDV/CL causes a *minimization* along factor I, still another difference between the two samples. The two small-eyed samples, however, show the same basic pattern: continued decreasing of the ratio NDV/CL, which first leads to maximization, then minimization, of the scores along factor I.

As the antagonistic effect of NLNS and NDV with CL are separately examined in factors II and III, their joint plot naturally separates the large- and small-eyed forms the best, and produces a pattern closely similar to that seen in the squared normalized data plotted on the ternary diagrams. This is most strikingly shown in the *birdsongensis* plot (fig. 14), where both groups show a tight positive correlation between factors II and III. A high ratio of NLNS/CL (II) shows a strong correlation with a high ratio of NDV/CL (III). Apart from the obvious effect of separating the two eye morphs, both morph clusters show the linear effect of ontogeny. The *raymondi* plot (fig. 15) shows much the same effect, although, as expected by now, ontogeny is less effectively portrayed in the large-eyed group.

The three intermediate specimens of *birdsongensis* shown on the ternary diagram (fig. 8) have interesting distributions on the three factor plots. In factor I versus factor II (fig. 11) they are

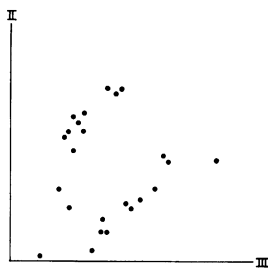


FIG. 14. Factor analysis plot for *P. logani birdsongensis*. Unrotated factors II and III.

associated with the small-eyed forms, while in factor I versus factor III (fig. 13) two of them group with the large-eyed forms, while the third is isolated from both clusters. This ambivalence is clearly shown in the third plot (factors II versus III; fig. 14), where the three are found between the two main clusters. In the third factor analysis, where all available specimens of *P. logani* were analyzed together, additional specimens (including the holotype) of *P. logani birdsongensis* were utilized. The plot of factors II versus III in this latter analysis (fig. 17) shows that three of the added specimens cluster with the intermediate group. The existence of a smaller, intermediate group may indicate the presence of a third discrete morph; in any case, Delo's (1940) observation that there seems to be intergradation between a "*logani*" and a "*hudsonicus*" eye type within the Birdsong *Phacops* is confirmed quantitatively.

The final factor analysis, of all three samples (a total of 75 specimens) is useful to compare relative distances and shapes of dispersion among all measurable *P. logani* available to me. The interpretations of the distributions of the factor scores are fundamentally the same as they are for *P. logani birdsongensis*, and need not be repeated here. The plot of factors I versus II (fig. 16) yields the familiar parabola, with the large-eyed *P. logani birdsongensis* occupying the apex. The small-eyed forms of *raymondi*, *birdsongensis*, and the holotype of "*P. hudsonicus*" cannot be distinguished, nor can large-eyed *raymondi* from all other *logani*. There are two groups—large-eyed and small-eyed—with large-eyed *P. logani birdsongensis* occupying the middle ground between them.

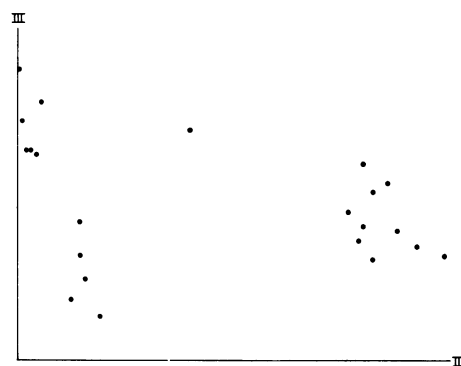


FIG. 15. Factor analysis plot of *Phacops logani raymondi*. Unrotated factors II and III

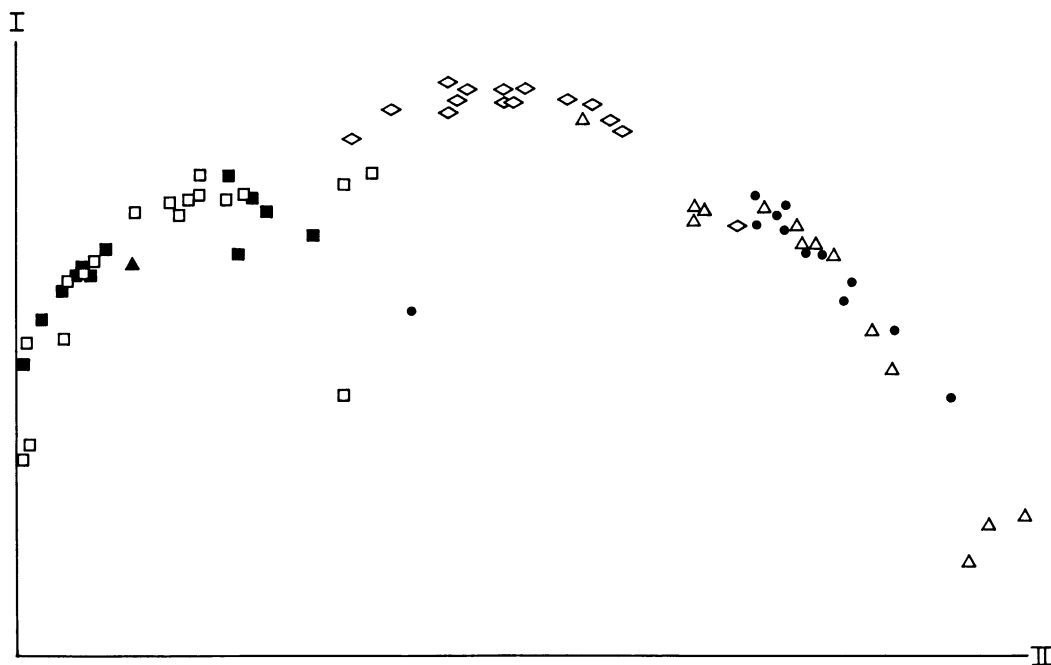


FIG. 16. Factor analysis plot of all mixed samples of *Phacops logani*. Unrotated factors I and II.

Symbols: □, small-eyed form, and ◇, large-eyed form, of *P. logani birdsongensis*; ■, small-eyed form, and ●, large-eyed form, of *P. logani raymondi*; ▲, small-eyed form, and △, large-eyed form, of Appalachian samples of *P. logani*.

Factor I versus factor III is not reported here, as the resultant graph fails to discriminate clearly any group save the large-eyed *birdsongensis*. Factors II versus III (fig. 17) already alluded to, again shows (1) strong dimorphism within subspecies, (2) the inseparability of the small-eyed forms, (3) the overlap between large-eyed *raymondi* and other *logani*, (4) the intermediate character of the large-eyed *birdsongensis*, (5) the third cluster of *P. logani birdsongensis* specimens, (6) the one intermediate *raymondi* specimen, and (7) the association of the holotype of "*Phacops hudsonicus*" with the third group of *P. logani birdsongensis*.

The significant within and among group variation in the degree and pattern of development of the eye polymorphism in *P. logani* aids materially in the delineation of discrete sub-taxa. It is noteworthy that, although factor analysis showed a greater tendency toward intergradation within the *birdsongensis* sample, the frequency histograms of NDV showed more overlap within the *raymondi* sample. Which of the patterns of polymorphism is primitive and which derived poses a seemingly insoluble

problem. Although eye morphology and polymorphism offer good criteria to add to the diagnoses of *P. l. raymondi*, *P. l. birdsongensis*, and *P. l. logani*, the relationships among the subspecies are more appropriately assessed on other criteria.

RELATIONSHIPS AMONG SUBSPECIES OF *PHACOPS LOGANI*

The five subspecies of *Phacops logani* recognized here each have a rather limited stratigraphic range (table 1); *P. l. raymondi* from the Gedinian (or perhaps lower Siegenian: see Boucot and Johnson, 1967) Haragan Formation of Oklahoma, and *P. logani birdsongensis* from the Ross Member of the Olive Hill Formation and the Birdsong Formation of Tennessee (Gedinian), were roughly coeval. *Phacops logani logani*, as understood herein, of the central and northern Appalachians, occurs in the lower Helderberg Group (principally the Gedinian Kalkberg-New Scotland sequence of New York and adjacent states) and in the Gedinian Roncelles Formation (or Roncelles Member of

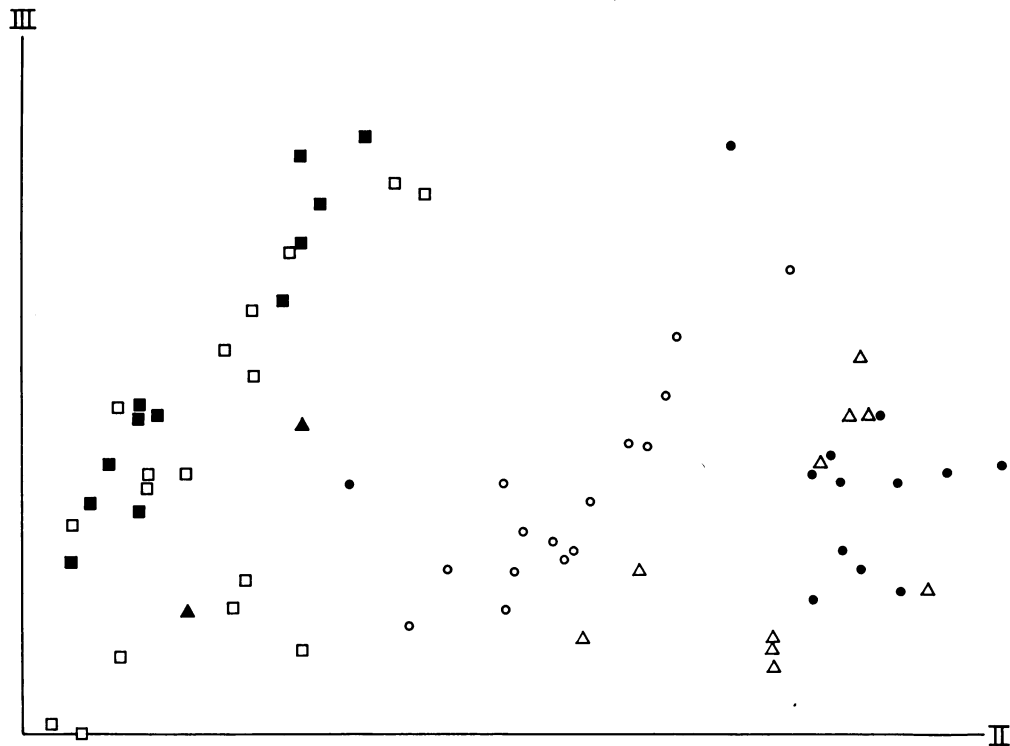


FIG. 17. Factor analysis plot of all mixed samples of *Phacops logani*. Unrotated factors II and III. Symbols: □, small-eyed form, and ○, large-eyed form, of *P. l. birdsongensis*; ■, small-eyed form, and ●, large-eyed form, of *P. l. raymondi*; ▲, small-eyed form, and △, large-eyed form, of Appalachian samples of *P. logani*.

the St. Albans Formation) and the Siegenian Cap Bon Ami Formation of Gaspé, Quebec. Samples from various Lower Devonian units of Maine and at Dalhousie, New Brunswick, (Clarke, 1909 [1908–1909]) attributed to *P. logani* were not examined. Specimens from the presumably Gedinnian Bailey Formation of Missouri cannot be assigned with confidence to any subspecies. *Phacops logani* has been reported from the Siegenian Becraft-Alsen-Port Ewen sequence of the upper Helderberg Group; only one specimen (from the Becraft Formation) was available to me and is referred to *P. logani* subspecies A. This is not to say, necessarily, that *P. l. logani* does not persist into the Siegenian other than in the Cap Bon Ami Formation. However, faunal lists are not to be trusted and additional (and well-preserved) specimens must be obtained from these units before the identity of *Phacops* in the upper Helderberg Group can be firmly established. The new subspecies *P. l. clarkei* to date is known only from the uppermost

Siegenian “Glenerie” Formation at Becraft Mountain, New York, and the Siegenian Murailles Formation at Percé, Quebec.

The first step in formulating a theory of relationships among these taxa is the recognition of characters which exhibit significant among-group variation, arranging such characters into morphoclines, and establishing their polarity (in terms of primitive and derived states). In this way, sister taxa can be identified in terms of shared-derived characters. Although more light is shed on primitive versus derived states (e.g., in eye morphology) when the other four species (*P. claviger* Haas, *P. clarksoni*, new species, *P. cristata* Hall, and *P. iowensis* Delo) are considered along with *P. logani*, there are characters of these five subspecies of *P. logani* germane to a discussion of their interrelationships to be considered at this juncture. The relationships among the five species are discussed toward the end of the present paper.

Small genal spines are almost always present

in *P. logani logani* and *P. l. clarkei*. They are rarely present in *P. l. raymondi* and apparently absent altogether in *P. l. birdsongensis*, in *P. logani* subspecies A, and in the rare small-eyed forms of *P. l. logani* of the central and northern Appalachians. Although genal spines are commonly seen in meraspid stages of *Phacops* and related genera, they are generally absent in adults, and their presence in the late holaspid stages of some *P. logani* should be considered a derived, albeit pedomorphic condition.

The postocular ridge developed on the fixigenal moiety of the ocular platform immediately anterior to the posterior marginal furrow is strongly developed externally in all these taxa, but is solid (leaving little trace on the internal mold) in *P. logani clarkei*, *P. logani* subspecies A, and in specimens from the Roncelles Formation. Although no good criteria exist to allow a firm judgment, lack of expression of this ridge on the internal mold is here considered to be derived. Similarly, the fixigenal and librigenal moieties of the ocular platform are more sharply differentiated (by the groove representing the trace of the obsolescent facial suture) in the Gedinnian taxa than in the later samples, and the former condition is here thought to be primitive.

Development of the intercalating ring, and degree of medial incision of glabellar furrow 1p, are important characters not only among the five subspecies of *P. logani*, but among all species of *Phacops* and related genera. The intercalating ring is present in all *P. logani*, and though variable even within populations, glabellar furrow 1p tends to be more deeply incised medially in *P. l. logani*, *P. l. birdsongensis*, and *P. l. raymondi* (especially the small-eyed forms) than in *P. l. clarkei* and *P. logani* subspecies A. Other genera (e.g., *Acernaspis* Campbell, *Ananaspis* Campbell) tend to show a well-developed intercalating ring, but glabellar furrow 1p is generally weakly incised medially. A strongly incised and continuous glabellar furrow 1p should then be considered advanced, although it is unclear whether Siegenian subspecies of *P. logani* (especially *P. l. clarkei*) retain a primitive expression of glabellar furrow 1p or instead exhibit an advanced (and secondary) tendency toward incorporation of the intercalating ring into the composite glabellar lobe (see discussion below).

The only ornamental feature of the cephalon that exhibits significant and consistent inter-

populational variation is the manner of tuberculation and granulation, particularly well shown on the composite glabellar lobe. The basic pattern of ornamentation in *P. logani* is a groundmass of small granules, which cover the larger tubercles and the spaces between them. This condition seems similar to that of *Ananaspis* Campbell. The morphocline from small granules (*Acernaspis*) to tubercles with superimposed granules (*Ananaspis*; the *P. logani* group) to smooth tubercles (other *Phacops* species) proposed by Campbell (1967, p. 29) seems plausible. The ornamentation in *P. logani clarkei* is particularly significant if Campbell's scheme is accepted, as the superimposed granules on the tubercles and those on the inter-tubercular areas have become extremely small and can only be detected under fairly high magnification. Thus, ornament in *P. l. clarkei* is herein considered to be derived with respect to the Gedinnian subspecies of *P. logani*.

The extremely variable (both inter- and intrapopulationally) nature of lens arrangement on the visual surface and the lack of comparable data for other related taxa make the systematic interpretation of dorsoventral file number and total lens number difficult. However, monomorphic patterns in number of dorsoventral files and overall number of lenses seem to be more generally the rule, and the almost 50–50 ratio of small-eyed versus large-eyed forms in *P. l. raymondi* and *P. l. birdsongensis*, seems to be a specialization. The variation is much less severe in other closely related taxa (*P. l. logani*) or entirely undocumented (*P. l. clarkei*). I tentatively conclude that the primitive condition of *P. logani* was something close to *P. l. logani* itself, i.e., many lenses arranged in 17 (rarely 18 or 19) dorsoventral files and the capacity to produce a small-eyed variant. *Phacops logani clarkei* shares with *P. l. logani* this

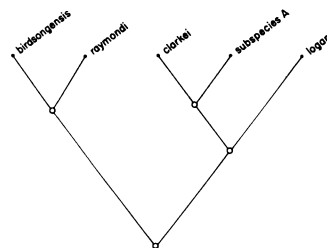


FIG. 18. Theory of relationships of subspecies of *Phacops logani*.

primitive feature. The large-eyed forms of *P. l. birdsongensis* generally share this primitive complement of dorsoventral files (albeit with fewer lenses on the average), whereas the eyes of *P. l. raymondi* are derived, with an average of only 16 dorsoventral files.

Common possession of similar but not identical dimorphism in similar ratios as well as other characters enumerated above leads to the following conclusions concerning relationships: *Phacops logani raymondi* and *P. l. birdsongensis* are sister taxa; *P. logani* subspecies A remains a difficulty, but is herein considered a sister taxon with *P. l. clarkei*. These two taxa in turn seem to form a natural sister group with *P. l. logani*, and these three, in turn, are the sister group of the *P. l. raymondi*-*P. l. birdsongensis* sister taxon. These relationships are diagrammed in figure 18.

REMARKS ON *PHACOPS CLAVIGER* HAAS, 1969

Phacops claviger from the Siegenian of Nevada was recently described by Winfried Haas (1969, p. 647). The specimens unfortunately were un-

available for examination for the present study. According to Haas's description and figures, however, it is clear that *P. claviger* is closely related to the *P. logani* group. Glabellar shape, ornamentation, morphology of the ocular platform and of the hypostoma seem identical in the two taxa. Similarly, the eye, although containing only 16 dorsoventral files, contains 77 lenses in the one specimen of *P. claviger* reported by Haas (1969, p. 647); this is within the range for *P. logani* but not for *P. cristata* or for *P. clarksoni*. The presence of a well-developed intercalating ring, although plesiomorphic for phacopids in general, alone precludes the assignment of this species to the *P. cristata* complex (see below). However, *P. claviger* is clearly unique in its staggered row of thoracic axial spines, and the large occipital spine is also unknown in *P. logani*. In addition, the genal spines of *P. claviger* are larger than any seen in *P. logani*. Although the relationships among all North American species of *Phacops* is considered at the end of the present report, it may be concluded at this point that *P. claviger* is a valid, distinct species of *Phacops* that forms a sister group with the entire *P. logani* complex.

PHACOPS CLARKSONI, NEW SPECIES

Figure 19

SEVEN CEPHALA, all apparently from the Schoharie Formation of the Schoharie Valley, New York, form the hypodigm for the new species *Phacops clarksoni*. No hypostomata, thoraxes, or pygidia can be assigned with any confidence to this new taxon. The cephala are all rather small (from 3.2 to 4.4 mm. long). These specimens are mosaic intermediates between the older *P. logani* (especially *P. l. clarkii*) and the *Phacops cristata* complex of the Emsian and Eifelian of North America. They

cannot, however, be assigned easily to either group.

DIAGNOSIS: A small species of *Phacops* with 17 dorsoventral files and more than 80 lenses in the eye. Lenses tending to protrude beyond interlensar sclera. Large genal spines present; no occipital spine or tubercle. Postocular ridge pronounced externally, reduced on internal mold. Intercalating ring generally wholly absorbed into composite glabellar lobe. Vincular furrow smooth, tending to become shallow anteromedially. Glabellar ornamentation with small tubercles only (granules absent).

Dorsal surface of composite glabellar lobe not steeply inclined anterodorsally in standard orientation. Composite glabellar lobe relatively flat, i.e., not inflated. Anterior margin of cephalon somewhat pointed, i.e., not smoothly rounded.

DESCRIPTION: This species possesses a remarkably flattened glabella and a high anterior arch in standard orientation. The genal spines are quite large with respect to cephalon size, and the occipital ring is covered with small tubercles, lacking a central node or spine. The postocular ridge is well developed on the external surface and solid, leaving no trace on the internal mold. The palpebral areas are smooth and gently curved. Glabellar lobes 1p are present distally as nodes. The intercalating ring is either wholly absorbed into the composite glabellar lobe, or is depressed, with the medial portion of glabellar furrow 1p generally obsolescent. Glabellar furrows 2p and 3p are sharply impressed (only known on the internal mold). Glabellar furrows 2p are inclined anteroproximally, reflecting the advanced (forward) position of the central portion of the intercalating ring. The glabella is lightly ornamented with small tubercles only. The lateral margins of the cephalon are ornamented with linear ridges.

The eyes have 17 dorsoventral files, with from 82 to 90 lenses per eye observed. The lenses tend to protrude beyond the interlensar sclera farther up each dorsoventral file than is common in most Phacopidae (see Eldredge, 1972a, p. 142). The area under the visual surface is devoid of ornament.

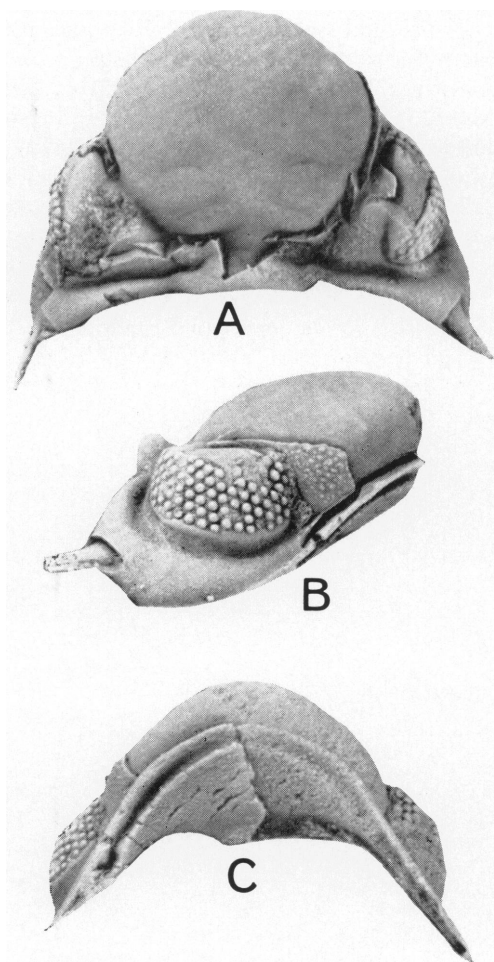


FIG 19. *Phacops clarksoni*, new species. Holotype, AMNH 29244, Schoharie Formation, New York. $\times 3$. A. Dorsal view. B. Right lateral view. C. Ventral view.

Ventrally, the vincular furrow has 10 notches posterolaterally. The notches are comprised of evaginations in both the proximal and distal walls. The vincular furrow tends to become rather shallow anteromedially. The anterior cephalic doublure is ornamented with granules anteromedially, which become elongate ridges posterolaterally. The hypostomal suture is straight (transverse).

Hypostoma, thorax, and pygidium unknown.

TYPE: Holotype, AMNH 29244.

MATERIAL EXAMINED: Seven cephalia in the collections of the American Museum of Natural History.

DISTRIBUTION: All seven specimens are apparently derived from the Schoharie Formation of east-central New York.

ETYMOLOGY: This species is named after the distinguished student of phacopid trilobites, Euan N. K. Clarkson.

REMARKS: The affinities of this species are summarized after the discussion of the *Phacops cristata* complex. There are few derived features unique to this species, but the particular combination of primitive and derived characters results in an entirely unique morphological pattern.

Phacops clarksoni resembles *P. logani*, especially *P. l. clarkei*, in the following features: (1) overall cephalic shape, especially relative flatness of the composite glabellar lobe; (2) tendency

toward obsolescence of the vincular furrow anteromedially; (3) eyes with 17 dorsoventral files each containing many lenses; and (4) smoothly curved palpebral area. It resembles *P. cristata* in having (1) large genal spines; (2) tendency to lose the intercalating ring by incorporation into the composite glabellar lobe; (3) absence of a postocular ridge on the internal mold; and (4) lack of microgranulation on the dorsal surface of the cephalon. Assessments of primitive versus derived states of these and other characters, and the relationships of *P. clarksoni* with other species, are discussed in another section.

The alternative possibility, that the seven specimens forming the hypodigm of *P. clarksoni* are in fact a large-eyed variant of *P. cristata*, must also be considered, particularly in view of the rarity of even possible examples of sympatry between two species of *Phacops* in the Devonian of North America. However, in all other cases of eye dimorphism reported on herein, the preponderance of other characters tends to unite the morphs into a single taxon. In this instance, other features, particularly the shape and thickness of the composite glabellar lobe, are so different between *P. clarksoni* and *P. cristata cristata* (the other phacopid taxon of the Schoharie Formation), that it is highly unlikely that these two phenae are dimorphs of the same species.

THE *PHACOPS CRISTATA* COMPLEX

SPECIMENS ASSIGNABLE to *Phacops cristata* as emended herein are found in Emsian strata in Quebec (Grande Grève Formation), New York (Esopus and Schoharie formations) and Ontario, and in Eifelian rocks primarily in Virginia, Pennsylvania, Ohio, New York, Ontario, Michigan, Indiana, and Alabama. Other occurrences, such as in the Camden chert (Eifelian) of Tennessee, are reported in the literature, and seem valid, although no well-preserved material from these units was available for the present study.

Phacops cristata as understood herein includes seven subspecies, reflecting an impressive radiation in a variety of environments. Well-documented samples are known from argillaceous shales, sandstones, siliceous limestones, pure limestones, and calcareous shales. The subspecies recognized are allopatric and to some extent allochronic. Although some of the taxa [e.g., *P. c. stummi*, new subspecies, and *P. c. canadensis* (Stumm)] are quite specialized and even aberrant members of the genus, other populations, especially from the Needmore shale of Virginia and Pennsylvania, and the Ragland sandstone of Alabama, conjointly termed *P. c. variabilis*, new subspecies, are quite conservative, retaining many features reminiscent of *P. logani*, and at the same time closely approximating *P. iowensis alpenensis* in some respects (see Eldredge, 1972b). Although it is not claimed that (1) *P. cristata* arose (as *P. c. variabilis*) directly from *P. logani* (e.g., *P. l. clarkei*) in the Appalachian region, or that (2) *P. iowensis alpenensis* arose from *P. cristata* (as, say, *P. c. variabilis*) in the Appalachian region, the occurrence of a relatively more primitive stock of *P. cristata* in the Appalachians suggests that the ancestral stock which gave rise to *cristata* and ultimately to *P. iowensis*, was probably situated in the eastern marginal seas. This conclusion is identical with that of an earlier paper (Eldredge, 1971b) wherein I claimed that two subspecies of *Phacops rana* (*P. r. rana* and *P. r. norwoodensis* Stumm) arose in the eastern margin of the cratonic sea in the Givetian. I have also argued (1972b) that *P. iowensis* also arose in the Appalachian region. In other words, although no claim is made that the samples I have

designated as *P. logani clarkei* were ancestral to those termed *P. cristata variabilis*, or that the *P. cristata variabilis* were ancestral to *P. iowensis alpenensis*, the three taxa (plus *P. clarksoni*) form a closely intergrading morphocline. Furthermore, whether or not *P. cristata variabilis* was in fact actually ancestral to *P. iowensis*, it was closer to the morphology of the hypothetical common ancestor of *P. cristata* and *P. iowensis* than were any of the other known subtaxa of *P. cristata*. The new, rather specialized taxa appearing in the continental interior in the Eifelian are herein interpreted as local, allopatric populations; populations to the east, particularly in the southern Appalachians, tended to remain conservative, but at the same time were the raw material for the origin of actual new species.

Hall and Clarke (1888, p. 18) established *P. cristata* var. *pipa* for small specimens mainly from the Onondaga Formation of New York. These specimens were distinguished from *P. c. cristata* by (1) smaller size, (2) smaller genal spines, (3) absence of axial spines on the occipital ring and axial rings of the thorax, (4) fewer "annulations" on the pygidium, and (5) fewer lenses in the eye. These are, indeed, significant differences between "*pipa*" and *P. c. cristata* from the Schoharie Formation. While establishing *P. cristata* var. *pipa*, Hall and Clarke (1888) also rejected Hall's (1861b) taxon *P. bombifrons* from the Onondaga Formation, claiming that the apparent lack of spines on the genae and occipital ring, and other differences with *P. cristata cristata*, were based on poor preservation of the Onondaga specimens. They referred (1888, p. 14) all *P. bombifrons* to *P. cristata cristata*. However, there is a major difficulty with this interpretation. Whereas some *P. cristata* with a well-developed series of axial spines are known from the Onondaga Formation, most well-preserved large specimens [in the AMNH Hall collections; I am unable to assign most of this material to the members described by Oliver (1954, 1956)] clearly lack the axial spines, and have only small genal spines. And, presence of axial spines is clearly variable on the intrapopulational level (see discussion of *P. c. variabilis* below). Furthermore the average number of lenses of the large Onondaga specimens is 48.4 (for 18 specimens),

with an observed range of 39–64. The comparable figures for 12 specimens of *P. cristata cristata* from the Schoharie Formation are mean: 71.5, and observed range: 48–81. Other differences between Onondaga and Schoharie samples of *P. cristata* emerge below. Suffice it to say, that there is enough data to differentiate the Emsian Schoharie Formation *P. c. cristata* from the Eifelian Onondaga Formation *P. cristata* in New York, but not enough to distinguish *P. bombifrons* Hall, 1861 from *P. cristata* var. *pipa*. I conclude that these last two taxa are synonyms, and that *P. c. bombifrons* has precedence. This is unfortunate in view of the fact that *P. cristata* var. *pipa* [or simply *P. pipa* in Stumm's (1954) usage] has become even more popular a name than *P. cristata*, and has been widely applied. Whichever name is in fact used, I do not recognize this taxon beyond New York State except in Ontario and Ohio. In addition to *P. cristata cristata*, *P. c. bombifrons*, *P. c. variabilis*, *P. c. stummi*, and *P. c. canadensis*, all mentioned above, I also recognize *P. c. gaspensis* (Clarke, 1908) from the Grande Grève and ?York River Formations of Quebec and, with some doubt, *P. c. nasutus* (Stumm, 1954) as valid. I was unable to obtain specimens sufficiently well preserved from the Esopus Formation at Highland Mills, New York. Usually considered *P. cristata* var. *pipa*, these specimens may ultimately prove more suitably referable to *P. logani*.

Phacops cristata Hall, 1861

- Phacops cristata* HALL, 1861b, p. 67
Phacops bombifrons HALL, 1861b, p. 67.
Phacops cristata: HALL AND CLARKE, 1888, p. 14, pl. 6, figs. 1–13, 16–29; pl. 8A, figs. 1–4.
Phacops cristata var. *pipa* HALL AND CLARKE, 1888, p. 18, pl. 8A, figs. 5–18
Phacops rana: KINDLE, 1912, p. 107, pl. 10, figs. 3, 4.
Phacops cristata: DELO, 1940, p. 16, pl. 1, figs. 4, 5.
non Phacops cristata: STUMM, 1954, pp. 212, pl. 4, figs. 8, 10.
Phacops pipa: STUMM, 1954, p. 213, pl. 4, figs. 1–6, 9, 11.
Phacops canadensis STUMM, 1954, p. 213, pl. 4, figs. 7, 15, 18.
Phacops nasutus STUMM, 1954, p. 214, pl. 4, figs. 12, 13, 16.
Phacops pipa: STUMM, 1964, p. 6, pl. 3, figs. 1–9, 11–15.

EMENDED DIAGNOSIS: An extremely variable species of *Phacops* exhibiting no within-population eye dimorphism. Eye generally with almost constant number of 14 dorsoventral files (*P.*

cristata cristata, *P. c. bombifrons*, *P. c. stummi*, *P. c. nasutus*) or exhibiting slight variation (*P. c. canadensis*, *P. c. gaspensis*, *P. c. variabilis*). Visual surface convex (“inflated”) dorsoventrally. A rudimentary lens generally present at dorsal margin of visual surface between sixth and seventh dorsoventral files. Palpebral area generally constricted (“pinched”) laterally, commonly tuberculate. Genal spines when present generally stout, long, slightly recurved posterodorsally; in some cases variably developed or absent (some *P. c. variabilis*) or seen only on internal mold without external expression (some *P. c. bombifrons*). Occipital ring variably with stout spine (especially *P. c. cristata*), with central tubercle, or smoothly granulate; occipital spine possibly absent even in specimens with thoracic spines (e.g., *P. c. variabilis*).

Postocular ridge generally well developed externally, not developed on internal mold. Intercalating ring depressed distally, medial lobe reflected anteriorly and incorporated into composite glabellar lobe (*P. c. cristata*, *P. c. canadensis*, *P. c. bombifrons*, *P. c. stummi*, *P. c. gaspensis*, *P. c. nasutus*) or variably absent or still present (*P. c. variabilis* only). Glabellar furrows 1p confluent with occipital furrow distally, then reflected anteromedially, becoming obsolescent medially. Glabellar furrows 2p strongly inclined anteroproximally. Composite glabellar lobe variably inflated or relatively flat, generally inclined anterodorsally at high angle in standard orientation. Glabella variably ornamented, most commonly with large tubercles only, in some cases with several size classes of tubercles present; in a few cases large tubercles showing signs of being formed by coalescence of smaller tubercles in “rosette”-like fashion.

Vincular furrow invariably deeply continuous anteromedially, with 10 or 11 posterolateral notches developed on both sides of the furrow wall. Hypostomal suture generally straight, in a few cases slightly convex anteriorly. Vincular furrow variably smooth or with granules anteromedially. Cephalic doublure ornament commonly granules medially, with some coalescence into wavy ridges anteriorly and laterally; one specimen of *P. c. cristata*, however, with entire doublure covered with wavy, somewhat disconnected ridges.

Hypostoma poorly known. In available specimens, seemingly short and broad, with continuous marginal furrow laterally and

posteriorly, and with only very short posterior projection. Central body somewhat convexly rounded. Maculae conspicuous, in anterolateral area of central body. Entire surface ornamented with granules in all specimens observed.

Thorax with axial spines (*P. c. cristata*) or with pronounced axial nodes (*P. c. stummi*) or with spines variably present or absent (*P. c. bombifrons*, *P. c. variabilis*) or unknown (*P. c. nasutus*, *P. c. canadensis*, *P. c. gaspensis*). Thoracic pleura notched posterodistally.

Pygidium with six, generally eight or nine axial rings plus terminal piece. Terminal piece not sharply demarcated from surrounding posterior pleural field. Six to eight pleura present, with interpleural furrows commonly developed on the anterior five pleura. Two or three (fused) articulating half rings present. Surface ornamented with tubercles.

TYPES: I herein designate NYSM 13883/1 as lectotype, and NYSM 13883/6 as paralectotype.

REMARKS: It is exceedingly difficult to compile a straightforward diagnosis of this taxon. The variation is real, however, and does not indicate a mixing of unrelated taxa, as specimens ranging the entire gamut of variation can be found in association, particularly at small exposures of the Needmore Formation in northwestern Virginia. Although the diagnosis embraces all observed variations, it would be as well to point out that virtually all common subspecies of *P. cristata* (*P. c. cristata*, *P. c. bombifrons*, *P. c. stummi*) have 14 dorsoventral files and are almost invariably without an intercalating ring. The variable development of the genal, occipital, and thoracic spines, however, has led to confusion in identifying this taxon, especially since their presence in *P. c. cristata* prompted Hall's choice of the specific nomen.

In the following treatment of the seven subspecies recognized herein, only differentia are listed in the diagnoses. Differences among these subspecies must be expressed as combinations of particular character states, because much overlap exists among them. A complete description is included only for *P. c. stummi*.

***Phacops cristata stummi*, new subspecies**

Figure 20

Phacops cristata var. *pipa* HALL AND CLARKE, 1888 (part), p. 18, pl. 8A, fig. 8 only.

Phacops pipa: STUMM, 1954 (part), p. 213, pl. 4, figs. 2-6, 9; not figs. 1, 11.

Phacops pipa: STUMM, 1964, p. 6, pl. 3, figs. 1-9, 11-15.

DIAGNOSIS: A subspecies of *P. cristata* with a monomorphic pattern of 14 dorsoventral files and an observed range of 25-56 lenses per eye. Genal spines short and stout; occipital spine absent. Intercalating ring almost entirely absent, present only medially as marked by faint curved pattern of glabellar furrow 1p at extreme postero-medial area of the composite glabellar lobe.

Composite glabellar lobe not highly inflated, but inclined fairly steeply in standard orientation. Genae almost vertical and large, creating very large anterior arch. Thorax with blunt axial tubercles.

DESCRIPTION: The composite glabellar lobe of this subspecies is composed of the anterior, 3p, 2p, and medial portion of the conjoined 1p glabellar lobes. The composite glabellar lobe is somewhat pointed anteromedially, and is relatively flat (i.e., not inflated). In standard orientation (with the dorsal margins of the visual surfaces in the same horizontal plane) the composite glabellar lobe is inclined antero-dorsally, and the frontal surface is vertical. The occipital ring is tuberculated and does not bear a medial spine or large tubercle.

The eye is large, extending from the axial furrow almost to the posterior border furrow, and reaching the height of the posterior region of the composite glabellar lobe. The visual surface is short (vertically), almost invariably containing 14 dorsoventral files, which are inclined anteroventrally in the anterior portion of the field, and are more nearly vertical in the central and posterior regions of the visual surface. From 25-56 lenses are found in each eye, marking a regular ontogenetic increase; however, the maximum number of lenses observed are not found in the largest specimens. There is usually a small (rudimentary) lens between the sixth and seventh dorsoventral files, immediately subjacent to the palpebral suture. The lenses do not protrude beyond the sclera, which is well developed between the lenses.

The visual surface is supported by a vertical "area under the visual surface," which is generally coarsely tuberculated; this area is inflected, rather sharply in the posterior region of the eye, into a gently sloping unornamented librigenal moiety of the ocular platform. This moiety is set off from the fixigenal moiety of the ocular platform by a groove marking the trace of the posterior ramus of the obsolescent facial suture. The fixigenal moiety forms a thin post-

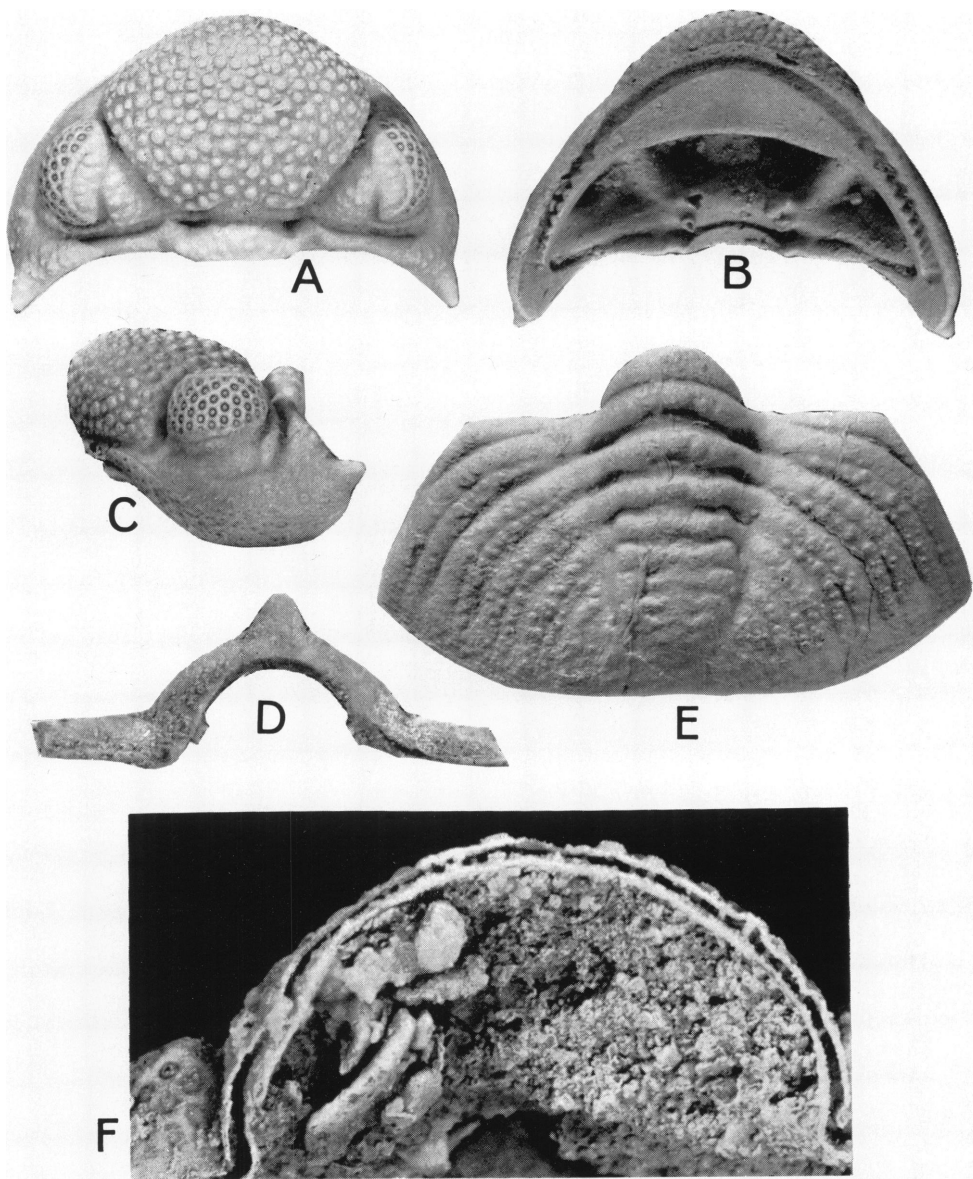


FIG. 20. *Phacops cristata stummi*, new subspecies. Jeffersonville Formation, Indiana. A-C. Holo-type cephalon, AMNH 28902. $\times 3$. A. Dorsal view. B. Ventral view. C. Left lateral view. D. Posterior view of a thoracic segment, UMMP 47209. $\times 4$. E. Pygidium, UMMP 47207. $\times 3$. F. Transverse sectional view of anterior glabellar lobe, showing inner and outer silicified layers, and interior tubules, representing canals opening as pores on the dorsal surface, UMMP 48591. $\times 9$.

ocular ridge, not developed internally, bounded by the posterior margin of the visual surface anteriorly, and the posterior marginal furrow posteriorly. The entire ocular platform is set off

from the gena by an anterior reflection of the posterior marginal furrow.

The genae are almost vertical and larger than in other species of *Phacops* (e.g., *P. rana*). In

standard orientation, the ventralmost portion of the cephalon is formed by an almost horizontal surface of the gena which extends from the region below the middle area of the eye back as far as the projection of the posterior margin of the occipital ring. The genae are strongly reflexed posterodorsally, and produced into a stout genal spine.

The palpebral area is confluent with the postocular ridge posterodistally, is moderately inflated, and is somewhat laterally compressed. It is set off sharply from the palpebral lobe by a distinct palpebral furrow. The palpebral lobe is kidney-shaped and inflated above the palpebral area.

The occipital ring is faintly divided into three (transverse) sections: two small distal regions set off by a faint ex-sagittal furrow, and a large central portion which has a straight posterior margin and is convex anteriorly. The deep linear depression anterior to the occipital ring is formed by the occipital furrow, which appears to be confluent with a continuous 1p glabellar furrow. This effect is created by the drastic reduction in height of the distal portions of the 1p glabellar lobes, and the incorporation of the medial portion of the intercalating ring into the composite glabellar lobe. Glabellar furrows 1p are strongly reflected anteroproximally and obsolescent at the midline. Glabellar furrows 2p are similarly inclined anteroproximally. Glabellar furrows 2p and 3p are variably implaced and in some cases absent.

The composite glabellar lobe is ornamented with tubercles of several size classes. Larger tubercles often have smaller tubercles (not granules) imposed upon them. A central depression, leading down through a pore canal seen on favorably preserved silicified specimens, occurs at the top of the larger tubercles (see fig. 20). The palpebral lobe, palpebral area, postocular ridge, and posterior border of the cephalon are also tuberculated. Large pores are distributed around the lateral and anterior margins of the cephalon.

Ventrally, the vincular furrow is complete and very deep anteromedially, unornamented, and with 11 notches grooved on both the proximal and distal walls. The cephalic doublure is ornamented with sparse granules medially, which become interconnected in wavy ridges posterolaterally, just anterior to the first notch of the vincular furrow.

The hypostomal suture is straight or slightly curved anteriorly. The hypostoma is unknown.

There are two pairs of cephalic apodemes associated with the occipital and 1p glabellar furrows. The 1p apodemes are massive, projecting downward and recurved posteroproximally. The occipital apodemes are smaller, and also recurved posteroproximally.

The thorax, known from isolated segments, is largely devoid of ornament, although tubercles appear on the distal portion of the posterior ramus of the pleuron. The axial ring bears a large, blunt spine. An ex-sagittal constriction in the anterodorsal portion of the axial ring (where the thoracic apodeme originates) creates a faint axial node which is not so well developed as in *P. logani logani*. The posterodistal tip of the pleuron is invaginated, forming a hook for insertion into the vincular notches of the cephalon.

The pygidium has six or seven axial rings plus a terminal piece that does not reach the posterior pygidial margin. The first two anterior ring furrows are evaginated, revealing (fused) articulating half rings. There are from five to seven pleura, with interpleural furrows developed on the anterior three, sometimes four, pleura. Tubercles occur on the axis and both rami of the pleura. The anterior five axial rings bear paired calluses, and axial rings 6–8 bear paired scars, for muscle insertion.

TYPES: Holotype, AMNH 28902; paratype, UMMP 47211.

MATERIAL EXAMINED: Approximately 135 specimens from the collections of the University of Michigan, Vanderbilt University, and the American Museum of Natural History. See Appendix for localities.

DISTRIBUTION: Rocks of Eifelian age of Michigan and Ohio and especially the Jeffersonville Formation of southern Indiana. See table 1.

ETYMOLOGY: This subspecies is named for the late Erwin C. Stumm who contributed much to our knowledge of the Devonian trilobites of the Midwest.

REMARKS: This subspecies is described in particular detail because of the availability of some 79 cephalia, 29 pygidia, and 17 isolated thoracic segments from the Jeffersonville limestone; each specimen is perfectly silicified, and many are completely unbroken, with both the external and visceral surfaces revealed. Many of the characters described are actually valid for the species as a whole, and some (e.g., cephalic

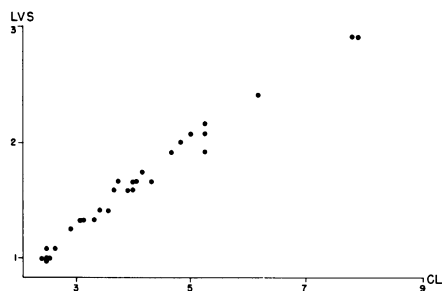


FIG. 21. Plot of LVS versus CL for *P. cristata stummi*. Note apparent instar clustering.

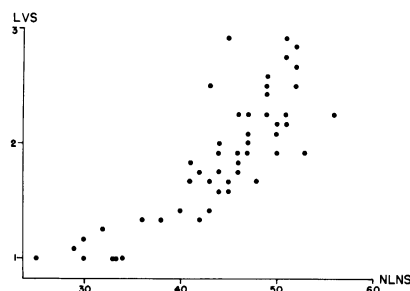


FIG. 23. Plot of LVS versus NLNS for *P. cristata stummi*.

apodemes) possibly for a larger taxon of phacopid trilobites.

According to Stumm (1964), these specimens all come from the Red Clay unit of the Jeffersonville Formation at the Falls of the Ohio River. This red clay is "a pockety layer ranging from 1 to 6 inches thick and intermittently developed along the bedding plane between the *Brevispirifer gregarius* beds and the overlying beds. The red clay apparently represents either an erosional interval at the top of the *B. gregarius* beds or a plane of solution and concentration of insoluble residues after lithification of the entire formation" (Stumm, 1964, p. 2). Although these specimens may have been reworked from a thicker stratigraphic unit and deposited together, lack of breakage and abrasion and the remarkable morphological homogeneity of this sample both seem to indicate that the sample represents a local population living over a fairly restricted time interval.

Many specimens with well-preserved eyes were available, affording a rare and welcome opportunity to study the ontogeny of the visual

surface of this species. Major dimensions, e.g., length of the visual surface (LVS) versus cephalic length (CL), show a linear, nearly isometric bivariate scatter (fig. 21), and possible successive molt stages are also apparent. Plots of total lens number (NLNS) versus CL (fig. 22) and NLNS versus LVS (fig. 23) show that lens addition is rapid in early ontogeny, slows down, and possibly becomes negative (indicating resorption) in later stages. No dimorphic pattern is apparent, nor was one found when these three variables were subjected to a factor analysis. The factor analysis for *P. c. stummi* was the same as that for *P. logani*, except LVS was included instead of NDV. The plot of factor I versus factor II (fig. 24) shows the familiar parabola, where factor I consists of high loadings on all three variables and factor II reflects antagonism between NLNS (strongly positive) and the other two variables (see table 4 for factor components). Factor II then, detects specimens which are not fully "maximized" along factor I because they either have more lenses in relation to cephalon size (high scores) or fewer lenses with respect to

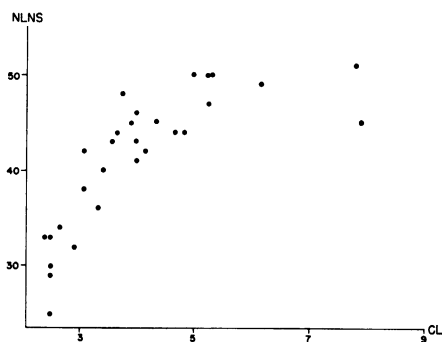


FIG. 22. Plot of NLNS versus CL for *P. cristata stummi*.

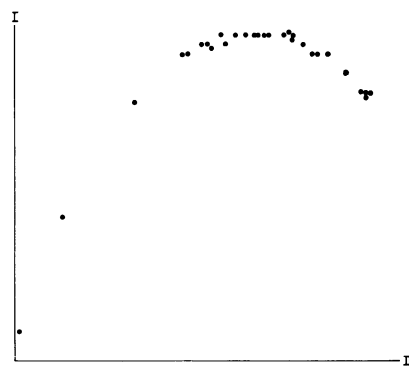


FIG. 24. Factor analysis plot for *P. cristata stummi*. Unrotated factors I and II.

TABLE 4
FIRST TWO FACTOR COMPONENTS FOR FACTOR
ANALYSIS OF JEFFERSONVILLE SAMPLE OF
Phacops cristata stummi

	N=29	
	I	II
CL	0.56	-.52
LVS	0.57	-.33
NLNS	0.61	0.79

Abbreviation: LVS, length of visual surface. For other abbreviations, see table 2.

TABLE 5
RAW DATA AND SUMMARY STATISTICS FOR THE FACTOR
ANALYSIS OF *Phacops cristata stummi*
(In micrometer units, where 6 units=1 mm.)

Specimen	CL	LVS	NLNS
1	63	23	50
2	94	35	51
3	63	26	50
4	58	24	44
5	74	29	49
6	30	12	25
7	56	23	44
8	41	17	40
9	50	21	42
10	35	15	32
11	29	12	33
12	40	16	36
13	37	16	42
14	43	17	43
15	30	12	33
16	63	25	47
17	52	20	45
18	48	20	43
19	95	35	45
20	37	16	38
21	30	13	29
22	60	25	50
23	30	12	30
24	48	19	41
25	32	13	34
26	48	20	46
27	45	20	48
28	47	19	45
29	44	19	44
\bar{X}	49.03	19.79	41.34
S_x	17.38	6.26	7.10
V	35.5	31.65	17.2

For abbreviations, see table 2.

cephalon size (low scores). As would be expected from inspection of the raw data, large specimens score low on both factors I and II, small specimens high on factor II but low on factor I, and intermediate specimens high on factor I and intermediate on factor II. But, apart from singling out the very smallest and very largest specimens, this plot only serves to show overall variation, and no clear plot of ontogeny similar to that seen in *P. logani birdsongensis* is to be found. Summary raw data and statistics for *P. cristata stummi* are given in table 5.

OTHER REFERRED SPECIMENS: A few specimens in the collections of the University of Michigan, Museum of Paleontology, from Eifelian rocks of Ohio and Michigan may also be referred to *P. cristata stummi*. None possesses an occipital spine and in general the intercalating ring is either almost or completely absent. Most are poorly preserved. All were labeled by E. C. Stumm as *Phacops pipa*, and they all conform to this general morphotype as originally defined by Hall and Clarke (1888). Among the valid subspecies approximating the "*pipa*-morphotype" these specimens fall closest, and are herein referred to *P. c. stummi*, although a specimen from the Columbus limestone of Ohio (UMMP 31322) resembles *P. c. canadensis* in glabellar shape and profile. Included in this group are specimens from the Bois Blanc Formation at Mackinaw City, Michigan, and one specimen from the Amherstburg dolomite, near Petersburg, Michigan.

Phacops cristata nasutus (Stumm, 1954)

Figure 25

Phacops nasutus STUMM, 1954, p. 214, pl. 4, figs. 12, 13, 16.

EMENDED DIAGNOSIS: Eyes with 14 dorsoventral files, with maximum of four to five lenses per dorsoventral file. Intercalating ring depressed, apparently not fully merged with composite glabellar lobe. Palpebral area laterally constricted. Vincular furrow deeply continuous anteriorly.

Composite glabellar lobe relatively flat, inclined moderately steeply anterodorsally in standard orientation. Anterior region of composite glabellar lobe produced, causing glabella to "overhang" even in standard orientation, and giving the glabella a marked pentagonal shape

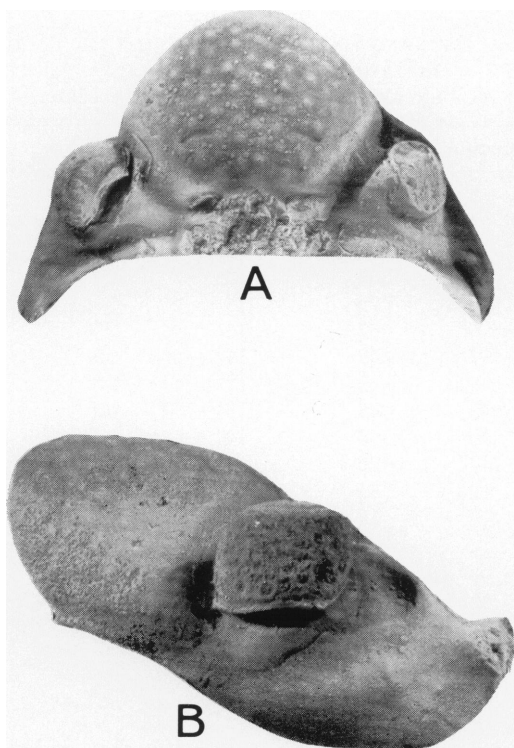


FIG. 25. *Phacops cristata nasutus* (Stumm, 1954). Holotype, UMMP 31329. Jeffersonville Formation, Indiana. A. Dorsal view. $\times 2$. B. Left lateral view. $\times 3$.

in dorsal aspect. Genal spines large, recurved posterodorsally.

Hypostoma, thorax, and pygidium unknown.

TYPES: Holotype, UMMP 31329; paratype, AMNH 29245.

MATERIAL EXAMINED: One specimen each from the UMMP and AMNH collections.

DISTRIBUTION: Jeffersonville limestone, southern Indiana.

REMARKS: This subspecies was originally based on a single internal mold of a cephalon from the Jeffersonville Formation. The posterior axial region of the cephalon is missing in this specimen. A second, somewhat larger and unlabelled cephalon was found in the G. K. Greene collection of the American Museum of Natural History. This second specimen also lacks the posterior axial region and the entire left eye and gena, but is otherwise closely similar to the holotype.

No stratigraphic data which might indicate which member of the Jeffersonville Formation produced these two specimens are available. Both are preserved in a light gray crystalline limestone, and are calcareous internal molds, precluding the possibility that they come from the same unit as did the sample of *P. c. stummi* discussed above. However, only the marked pentagonal shape of the glabella of *P. c. nasutus* offers a distinct difference between this subspecies and *P. c. stummi*, and for this reason *P. c. nasutus* is recognized only with some hesitation herein.

Phacops cristata canadensis (Stumm, 1954)

Figure 26

Phacops canadensis STUMM, 1954, p. 213, pl. 4, figs. 7, 15, 18.

Phacops pipa: STUMM, 1954 (in part), p. 213, pl. 4, fig. 11 only.

EMENDED DIAGNOSIS: Cephalon as for *P. cristata stummi* except composite glabellar lobe quite broad, short, and gently rounded anteriorly. In standard orientation, composite glabellar lobe steeply inclined anterodorsally. Anterior arch very large.

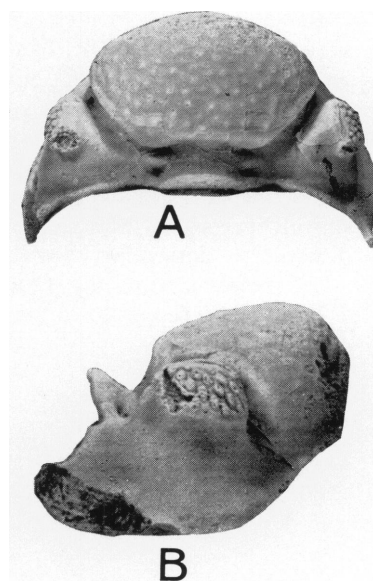


FIG. 26. *Phacops cristata canadensis* (Stumm, 1954). Lower Onondaga Formation, Port Colborne, Ontario. Holotype cephalon, UMMP 31327. A. Dorsal view. $\times 2$. B. Right lateral view. $\times 3$.

Genal spines large; no occipital spine or node observed. Eye small, with 11, 13, or 14 dorsoventral files (mean: 13), and from 17 to 40 lenses (mean approximately 30).

Hypostoma unknown. Thorax apparently without axial nodes or spines. Thorax and pygidium poorly preserved in available material, apparently similar to *P. cristata stummi*.

Types: Holotype, UMMP 31327; paratype, UMMP 31328.

MATERIAL EXAMINED: Twenty-four specimens from the UMMP collections.

DISTRIBUTION: "Lower Onondaga limestone," Port Colborne, Ontario. See Appendix.

REMARKS: This is perhaps the most aberrant taxon of *Phacops* in North America. All specimens are preserved as dolomitized internal molds. The extremely steep slope of the glabella, and its short, broad shape seem derived; the small eyes, with a variable number of dorsoventral files and small number of lenses, are likewise extreme developments, closely resembling only the eyes of *P. cristata gaspensis*.

An inspection of raw data (fig. 27; table 6) shows one small specimen with very few lenses and only 11 dorsoventral files. Then six specimens follow which exhibit no real increase in NLNS as they increase CL. All these specimens have 13 dorsoventral files. Four larger specimens, each with 14 dorsoventral files in each eye, show a marked increase in NLNS, while, of the two large specimens with 13 dorsoventral files, one shows a drop, and the other a constant value, in NLNS. Whether this plot exhibits dimorphism or, perhaps more likely, a (?pedomorphic) deviation from the "normal" *cristata* pattern, where four specimens ultimately do show the expected pattern is difficult to determine. Small specimens of *P. c. bombifrons* from the Onondaga limestone of New York resemble larger speci-

TABLE 6
RAW DATA AND SUMMARY STATISTICS FOR THE FACTOR
ANALYSIS OF *Phacops cristata canadensis*
(In micrometer units, where 6 units = 1 mm.)

Specimen	CL	NDV	NLNS
1	71	13	28
2	50	13	21
3	52	14	40
4	34	13	29
5	29	13	30
6	67	14	39
7	47	14	39
8	45	12	28
9	41	13	30
10	50	14	33
11	28	13	26
12	41	13	27
13	18	11	17
\bar{X}	44.08	13.08	29.77
S_x	14.94	0.86	6.80
V	33.9	6.6	22.8

For abbreviations, see table 2.

mens of *P. c. canadensis*, adding further evidence that this subspecies is a pedomorphic derivative from the main *P. cristata* stock.

A factor analysis similar to the treatment given the subspecies of *P. logani* was performed on 13 specimens of *P. cristata canadensis*. Components are given in table 7. Factor I versus factor II (fig. 28) yields a parabolic distribution, where factor I again reflects a "maximization" or "balancing" effect among the three variables (CL, NDV, NLNS), and factor II, which reflects an antagonistic effect between CL and NDV, determines deviation from the maximization along the parabola. The plot corresponds very closely to ontogeny (as determined by CL). Early in ontogeny, maximization along factor I is increased by holding dorsoventral file addition constant as CL increases. In later stages, dorsoventral file addition ceases as the head grows, and scores decrease correspondingly along factor I. A high score along factor III denotes a relatively greater proportion of lenses with respect to the other two variables, especially NDV. When factor III is plotted against factor I (fig. 29), a linear array (a one-sided parabola, with the exception of one specimen) results. Both small and large specimens disturb maximization of the three variables

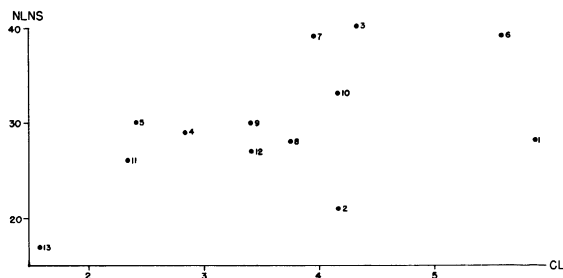


FIG. 27. Plot of NLNS versus CL for *P. cristata canadensis*.

TABLE 7
FACTOR COMPONENTS FOR FACTOR ANALYSIS OF
Phacops cristata canadensis

	N=13		
	I	II	III
CL	0.55	0.80	-.25
NDV	0.61	-.59	-.53
NLNS	0.57	-.13	0.81

For abbreviations, see table 2.

because at both ends of the ontogenetic sequence, there is a relatively greater number of lenses in proportion to the number of dorsoventral files.

Factor II versus factor III (fig. 30) yields a plot very similar to the raw data plot of CL and NLNS alone. Among specimens where NDV remains 13, a more marked tendency to reduce the proportion of NLNS to NDV is shown than in the plot of raw data. The analysis still leaves the problem of dimorphism open, however.

In sum, *P. cristata canadensis* is a highly unusual, specialized taxon closely related to *P. c. stummi*, but nevertheless easily distinguished from that subspecies. I have seen no specimens other than those from Port Colborne, Ontario, which may be referred to *P. c. canadensis* with the possible exception of a single cephalon (UMMP 31322) from the Columbus limestone of Ohio.

Phacops cristata bombifrons (Hall, 1861)
Figures 31, 32

Phacops bombifrons HALL, 1861b, p. 67.

Phacops bombifrons: HALL, 1876, pl. 6, figs. 18–29.

Phacops cristata: HALL AND CLARKE, 1888 (in part), p. 14, pl. 6, figs. 11, 17–25, 28; not figs. 1–10, 12, 13, 26, 27, 29; not pl. 8A, figs. 1–4.

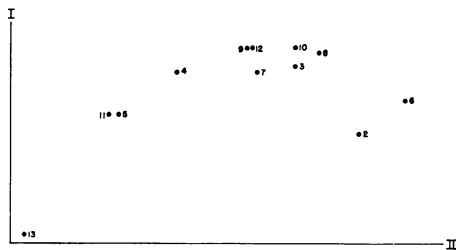


FIG. 28. Factor analysis plot for *P. cristata canadensis*.
Unrotated factors I and II.

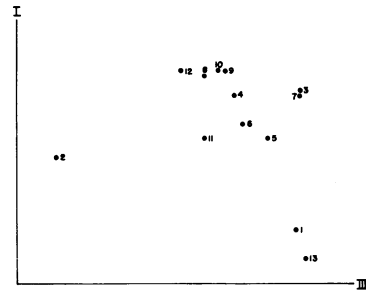


FIG. 29. Factor analysis plot for *P. cristata canadensis*.
Unrotated factors I and III.

Phacops cristata var. *pipa* HALL AND CLARKE, 1888 (in part), p. 18, pl. 8A, figs. 5–7, 9–18, not fig. 8.

Phacops cristata var. *pipa*: DELO, 1940 (in part), p. 17, pl. 1, figs. 6, 7.

EMENDED DIAGNOSIS: Eyes with 14, rarely 13, 15, or 16 dorsoventral files, and from 39 to 64 lenses per eye observed. Visual surface convex dorsoventrally. Area under visual surface high, coarsely tuberculated.

Genal angles usually with short spines, in some cases not expressed externally. Occipital ring without spine, in some cases with median tubercle or node. Intercalating ring variably present in small specimens, usually wholly absorbed into the composite glabellar lobe in larger specimens. Glabella moderately inflated, usually not steeply inclined anterodorsally in standard orientation. Cephalic doublure generally ornamented with sparse tubercles anteromedially, becoming connected into wavy ridges posterolaterally.

Thorax with axial spines or nodes usually absent, although sometimes present. Pygidium as for species.



FIG. 30. Factor analysis plot for *P. cristata canadensis*.
Unrotated factors II and III.

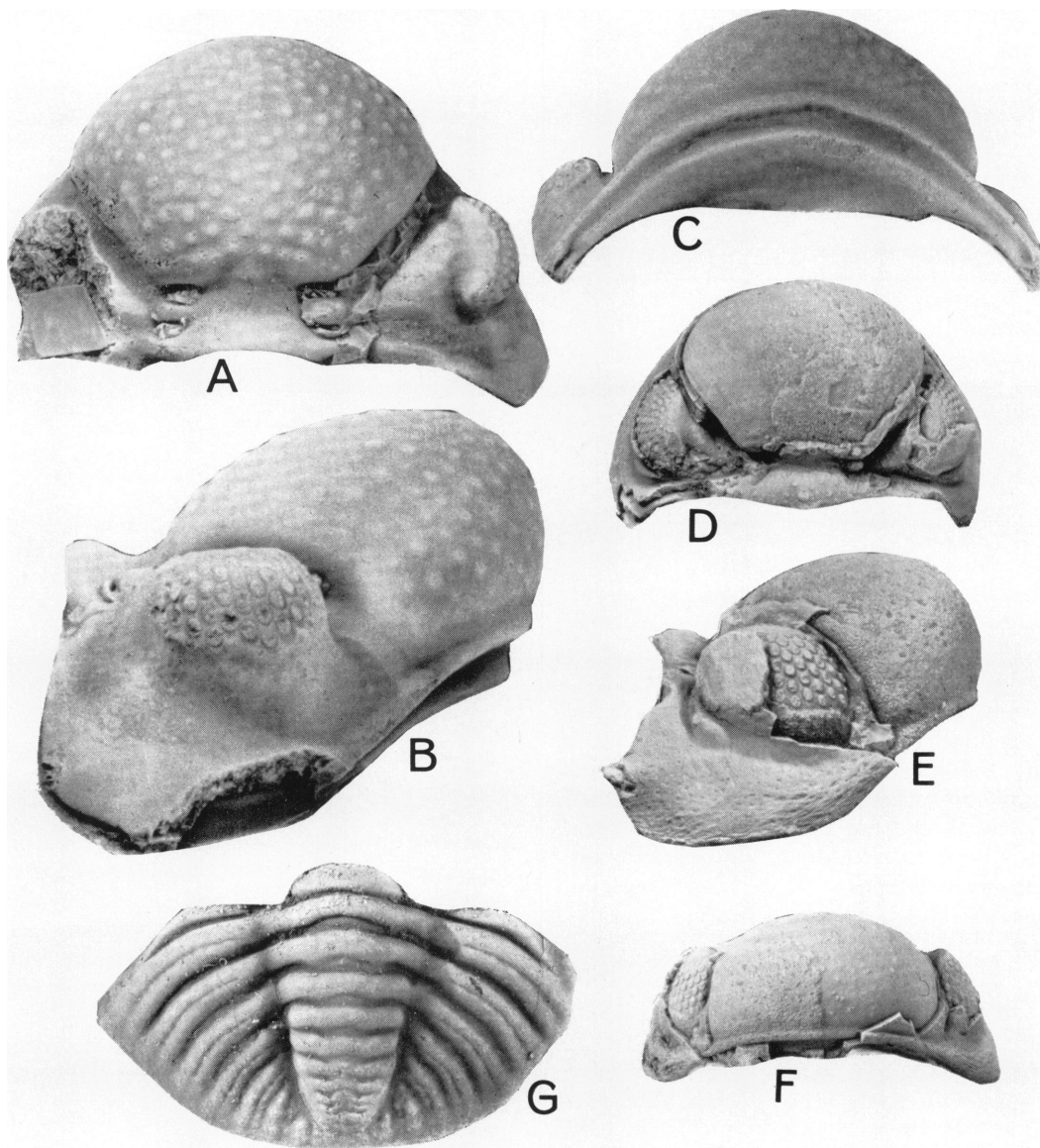


FIG. 31. *Phacops cristata bombifrons* (Hall, 1861). A–C. Lectotype, AMNH 4071/2A. A. Dorsal view of cephalon. $\times 2$. B. Right lateral view. $\times 3$. C. Oblique ventral view. $\times 3$. D–F. AMNH 4071/1. D. Dorsal view. $\times 2$. E. Right lateral view. $\times 3$. F. Frontal view. $\times 2$. Note faint trace of circular (*phacopid*) pattern of muscle scars on extreme left portion of anterior glabellar lobe. G. Pygidium, NYSM 13884/4. $\times 2$.

TYPES: I herein designate AMNH 4071/2A as lectotype, and AMNH 4071/1 as paralectotype. These are among those specimens illustrated in Hall, 1876, pl. 6, figures 28, 29 (AMNH 4071/1) and figures 22–25 (AMNH 4071/2A), the only time Hall ever figured *Phacops bombifrons*. These types were later refigured as *Phacops cristata* by

Hall and Clarke, 1888, pl. 6, figures 24, 25 (AMNH 4071/1) and figures 16, 17, 21, 23 (AMNH 4071/2A).

MATERIAL EXAMINED: Approximately 125 specimens in the collections of the New York State Museum and the American Museum of Natural History. See Appendix for localities.

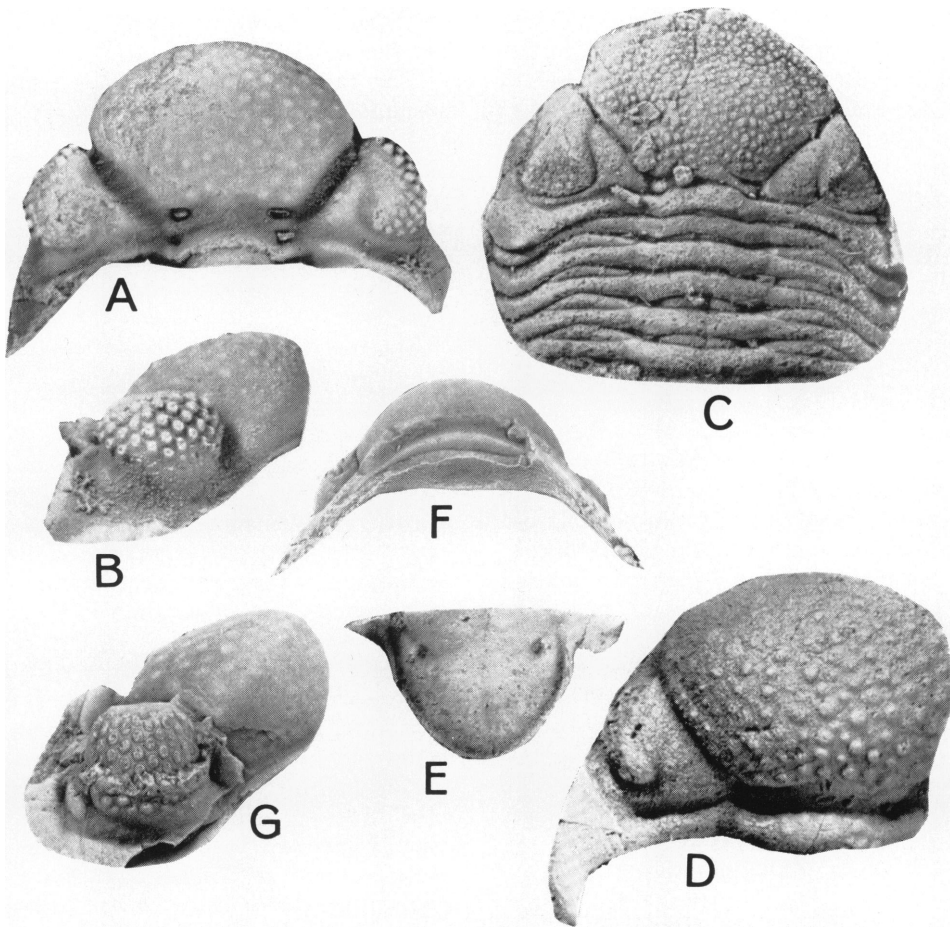


FIG. 32. *Phacops cristata bombifrons* (Hall, 1861). A-E. Three specimens figured by Hall and Clarke (1888) as *Phacops cristata* var. *pipa*. A, B, E. NYSM 13884/8. $\times 5$. A. Dorsal view of cephalon. B. Right lateral view. E. Associated hypostoma. C. NYSM 13884/2, latex cast of cephalon and anterior five thoracic segments. $\times 3$. D. NYSM 13884/3, dorsal view of cephalon. $\times 3$. F. AMNH 4071/4, ventral view, showing ornament of cephalic doublure. $\times 2$. G. AMNH 29253, right lateral view showing tubercles resembling lenses immediately subjacent to visual surface. $\times 3$.

DISTRIBUTION: Onondaga limestone of New York and its equivalents in Ontario and Ohio; see table 1.

REMARKS: The *nomen* "*bombifrons*" has been resurrected because the types of *Phacops cristata* var. *pipa* fall within the observed range of morphological variation of the larger "*P. cristata*" (= *P. bombifrons*) of the Onondaga limestone of New York. Reduction of spinescence, smaller eyes with fewer lenses, a tendency for smaller specimens to retain a distinct intercalating ring, and retention of granular ornamentation on the

anterior cephalic doublure are the primary differences between *P. cristata bombifrons* and *P. c. cristata*. These two subspecies, however, share a characteristic tumid profile of the composite glabellar lobe, and a relatively lower anterior arch than all other subspecies with the exception of *P. c. variabilis*. It is significant that, in terms of most of those characters which differentiate *P. c. bombifrons* from *P. c. cristata*, *P. c. bombifrons* is the more primitive, despite the fact that it is stratigraphically younger than *P. c. cristata*.

Several specimens of *P. c. bombifrons* show an irregular ventral margin of the visual surface (fig. 32). In most cases, large tubercles occupy the position where lenses might be expected to be found. Sectioning of such specimens, however, has not revealed any traces of lens structure. Nevertheless, subspecies of *P. cristata* with relatively few lenses per dorsoventral file frequently develop callus-like thickening on the area under the visual surface. This is especially noticeable in those specimens with an irregular lower border to the visual surface. My tentative interpretation of this condition is that populations with relatively few lenses per dorsoventral file are apomorphic, and *P. cristata* with many lenses are primitive. The reduced number of lenses per dorsoventral file appears to result from loss of lenses (not necessarily during holaspis ontogeny) from the bottom of the visual surface.

One other morphological feature encountered in *P. c. bombifrons* is worthy of mention. The paralectotype (AMNH 4071/1), figured by Hall and Clarke (1888, pl. 6, figs. 24, 25) from the "Onondaga" limestone of Ontario, offers the only well-preserved field of muscle scars on the anterior glabellar lobe that I have seen for any of the species treated in this study (fig. 31). The pattern is typically "phacopid" (Eldredge, 1971a) and not unlike that of *Phacops rana*.

Phacops cristata cristata Hall, 1861

Figure 33

Phacops cristata HALL, 1861b, p. 67.

Phacops cristata: HALL AND CLARKE, 1888 (in part), p. 14, pl. 6, figs. 1–10, 12, 13, 26, 27, 29; pl. 8A, figs. 1–4; not pl. 6, figs. 11, 17–25, 28.

Phacops cristata: DELO, 1940, p. 16, (in part), pl. 1, figs. 4, 5.

EMENDED DIAGNOSIS: Cephalon with large genal spines (for genus) and, frequently, with an occipital spine. Intercalating ring depressed distally, entirely incorporated into composite glabellar lobe medially. Glabella inflated dorsoventrally; slope of glabella progressively more horizontal through holaspis ontogeny (in standard orientation). Visual surface tall, with from 48–81 lenses observed (mean: 71.5) with up to six lenses per dorsoventral file. Eye with monomorphic pattern of 14 dorsoventral files.

Vincular furrow with 11 notches, developed in both inner and outer walls. Ornament of cephalic doublure variably granules medially,

intergrading into wavy ridges laterally, or wavy transverse ridges entirely.

Thorax with axial spines or nodes on all specimens observed.

TYPES: As for species.

MATERIAL EXAMINED: Approximately 60 specimens from the collections of the New York State Museum and the American Museum of Natural History. See Appendix for localities.

DISTRIBUTION: Schoharie Formation, New York State.

REMARKS: This subspecies is confined to the Schoharie Formation of New York State. Smaller specimens, including NYSM 13883/4 figured by Hall and Clarke (1888, pl. 6, figs. 6, 7) resemble *P. c. stummi* and *P. c. canadensis* in glabellar profile (i.e., glabellar strongly inclined anterodorsally forming a high anterior arch). In larger specimens, the composite glabellar lobe becomes more horizontal, but remains relatively more tumid ("inflated") than in *P. c. stummi* or *P. c. canadensis*.

Only four thoraxes were observed. All possess the well-known series of axial spines. It remains a possibility, however, that development of these spines may be variable as in *P. c. bombifrons* and *P. c. variabilis*. Although *P. cristata cristata* is the only subspecies with a well-developed occipital spine, I have seen specimens clearly lacking this feature on both external and internal molds. So, even within *P. cristata cristata* itself, development of spines is variable, though not nearly so much so as in other subspecies.

Phacops cristata variabilis, new subspecies

Figure 34

Phacops rana: KINDLE, 1912, p. 107, pl. 10, figs. 1–5.

Phacops cristata: KINDLE, 1912, p. 107, pl. 10, figs. 6–8.

Phacops cristata var. *pipa*: KINDLE, 1912, p. 108, pl. 10, figs. 9, 10.

DIAGNOSIS: Eyes with 14, 15, or 16 dorsoventral files, with variable number of lenses not producing dimorphic pattern. Visual surface rather flat (dorsoventrally) for species. Genal spines in some cases present, especially on smaller specimens. No occipital spine or median tubercle. Intercalating ring variably heavily tuberculated medially, frequently complete, but occasionally entirely merged with composite glabellar lobe. Glabellar furrow 1p variably distinct or obsolescent medially.

Composite glabellar lobe not highly inflated, inclined anterodorsally in smaller specimens, becoming more horizontal in larger specimens. Palpebral area variably gently rounded or constricted ("pinched") transversely.

Tubercles on glabella bluntly rounded, of two size classes, larger tubercles vaguely rosette-like. Large tubercles on area under visual surface, palpebral lobe, palpebral area, occipital ring.

Notches on vincular furrow 11, not always

developed on distal wall. Cephalic doublure with disconnected granules medially, becoming wavy ridges posterolaterally.

Thorax generally without medial axial spines or tubercles; large axial spines in some cases developed. Distal tips of pleura weakly notched. Pygidium in some cases with axial node on first (anterior) axial ring, generally with nine axial rings and terminal piece, with interpleural furrows developed on anterior four or five pairs

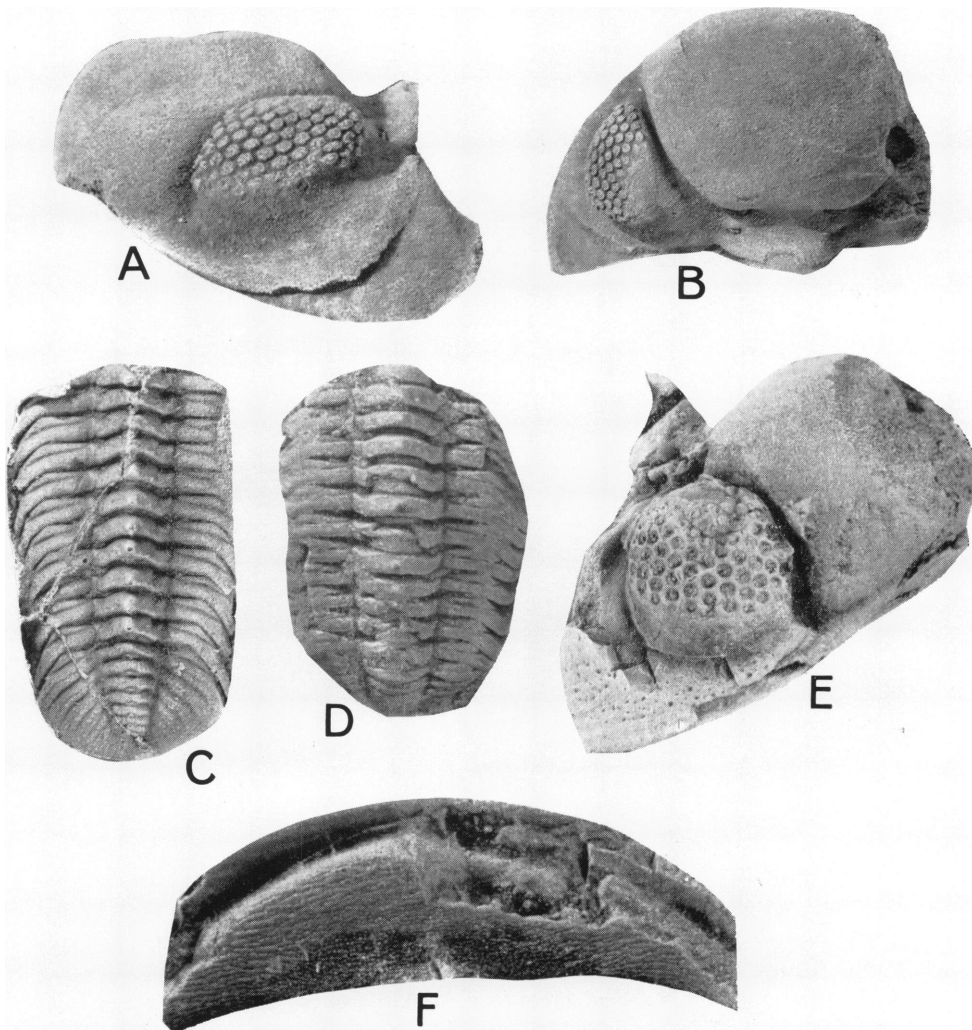


FIG. 33. *Phacops cristata cristata* Hall, 1861. Schoharie Formation, New York. A, B. Lectotype, NYSM 13883/1. A. Left lateral view. $\times 3$. B. Dorsal view. $\times 2$. C. AMNH 2892/2, latex cast of thorax and pygidium. $\times 1.5$. D. NYSM 13883/6, thorax showing only small axial tubercles. $\times 3$. E, F. Columbia University 3938. E. Right lateral view of cephalon, showing large occipital spine. $\times 3$. F. Ventral view showing ornament of cephalic doublure. $\times 6$.

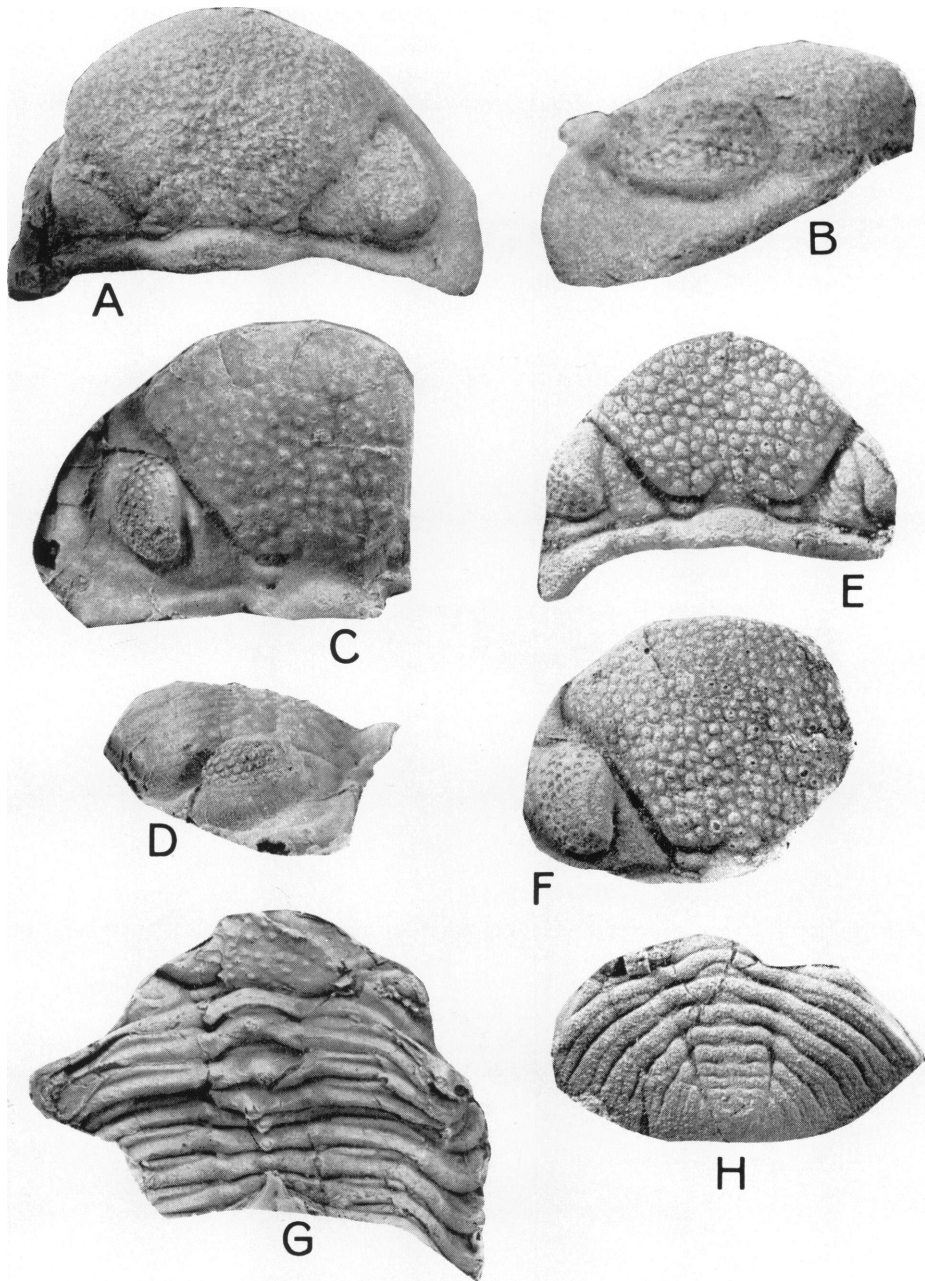


FIG. 34. *Phacops cristata variabilis*, new subspecies. A, B. Holotype cephalon, USNM 62132. Needmore Formation, Pennsylvania. A. Dorsal view. $\times 3$. B. Right lateral view. $\times 4$. C, D. Internal mold, Ragland Formation, USNM Collection. C. Dorsal view. $\times 2$. D. Left lateral view. $\times 2$. E, F. Two latex casts of external molds showing variation in development of the intercalating ring. Ragland Formation, USNM Collection. $\times 2$. G. Latex cast of posterior region of cephalon and anterior region of thorax, showing axial spines on thoracic axial rings only. Needmore Formation, AMNH 29254, AMNH loc. 3098. $\times 2$. H. Cast of external mold of pygidium, Ragland Formation, USNM Collection. $\times 2$.

of pleura. Tuberculation most heavily developed on posterior moiety of pleuron (i.e., posterior to interpleural furrow.)

TYPES: Holotype, USNM 62132; paratype, AMNH 29246.

MATERIAL EXAMINED: Approximately 165 specimens in the collections of the National Museum of Natural History and the American Museum of Natural History.

DISTRIBUTION: Needmore Formation of southern Pennsylvania, Virginia, and West Virginia; Ragland Formation of Alabama. See Appendix for localities.

ETYMOLOGY: The name refers to the great amount of intra-populational variability exhibited by this subspecies.

REMARKS: The sample from the Ragland Formation exhibits far less variability than the Needmore samples. In the Ragland, 12 of 13 eyes studied had 14 dorsoventral files. In addition, this sample displayed little variability in having the intercalating ring generally well developed, and no thoracic axial spines were encountered. The remarks in Eldredge (1972b) concerning the Ragland taxon hold, although they were based on a different sample not available for reexamination for the present study.

The possibility that presence or absence of thoracic axial spines may in fact be (sexually) dimorphic must be considered. However, the two localities in the Needmore of Virginia sampled for this study show greatly different proportions of spined versus non-spined thoraxes (virtually none at AMNH loc. 3099; 40–50 percent spined at AMNH loc. 3098). At present, it seems wise simply to think of spine development as variable both within and among population samples.

Although the Ragland and Needmore *Phacops cristata* can be distinguished from each other, they are “sister” populations and I can see no reason to name them separately. Their relationships with other subspecies of *P. cristata* are discussed below.

Phacops cristata gaspensis (Clarke, 1908)

Figure 35

Phacops logani var. *gaspensis* CLARKE, 1908 (1908–1909), p. 119, pl. 10, figs. 5, 6, 10–15; not fig. 16.

Phacops logani var. *gaspensis*: DELO, 1940, p. 20, pl. 1, figs. 10–12.

EMENDED DIAGNOSIS: Eyes with 12–14 dorsoventral files, the smaller specimens in general

with fewer dorsoventral files. Visual surface convex dorsoventrally. Palpebral area laterally constricted. Number of lenses per dorsoventral file variably small (e.g., two or three lenses in central dorsoventral files) or moderate (e.g.,

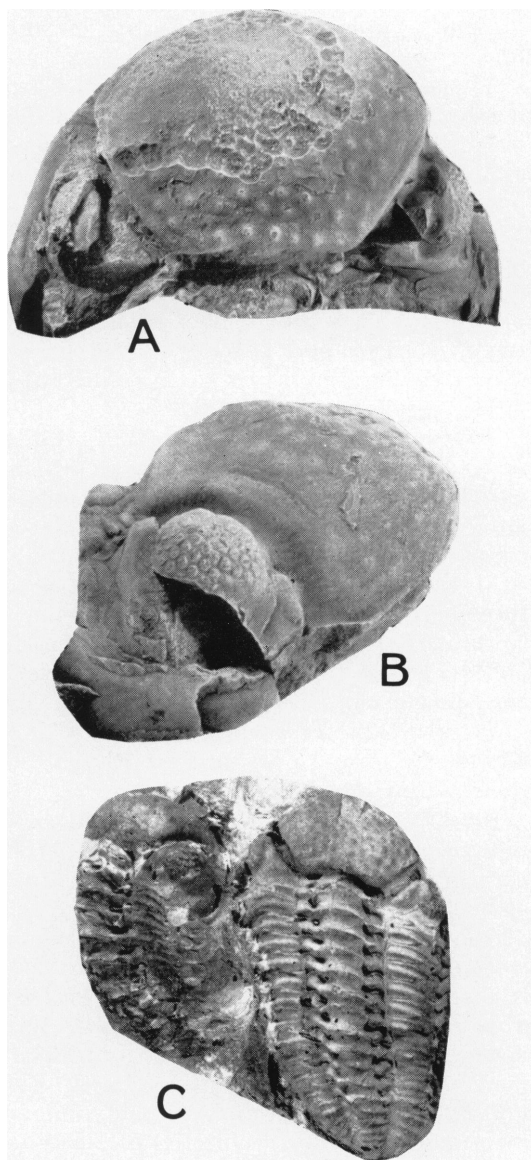


FIG. 35. *Phacops cristata gaspensis* (Clarke, 1908). A, B. Lectotype cephalon, NYSM 13885e/3, Grande Grève Formation, Gaspé, Quebec. A. Dorsal view. $\times 2$. B. Right lateral view. $\times 1.5$. C. Portion of slab showing two specimens figured by Clarke (1908), NYSM 13885e/2, Grande Grève or York River Formation. $\times 1.5$.

four or five lenses). Genal spine small or absent; no occipital spine or node. Intercalating ring variably present, rarely wholly absorbed into composite glabellar lobe. Composite glabellar lobe moderately inflated, inclined at a moderate (for species) angle anterodorsally. Composite glabellar lobe with large tubercles, with traces of "rosette" pattern of smaller tubercles superimposed on larger tubercles.

Vincular furrow with 10 or 11 notches, with notching developed in both proximal and distal walls. Anterior cephalic doublure with sparse granules, becoming elongate but not connected into wavy ridges posterolaterally.

Thorax apparently without axial spines; axial nodes present near axial furrow on internal mold. Thorax only lightly tuberculated.

Pygidium with about eight axial rings plus terminal piece, and generally seven pairs of pleura, with from three to five interpleural furrows on the anterior pleura.

TYPES: Clarke (1908 [1908–1909]) did not designate a holotype. A lectotype, NYSM 13885e/3, is herein designated. The specimens associated on a single slab (NYSM 13885e/2) are paralectotypes.

MATERIAL EXAMINED: Approximately 48 specimens from the American Museum of Natural History, the New York State Museum, and the Université de Montréal were available. See Appendix for localities.

DISTRIBUTION: This subspecies occurs in the Grande Grève and possibly York River formations, of the Gaspé Peninsula, Quebec.

REMARKS: Clarke (1908 [1908–1909]) referred this taxon to *Phacops logani*, but the morphology of the eyes and posterior region of the glabella clearly ally this taxon with *P. cristata*. The larger cephalon (NYSM 13885e/3) figured by Clarke (1908 [1908–1909], pl. 10, figs. 11–13) is almost identical with typical *P. c. bombifrons* from the Onondaga limestone of New York; however, smaller specimens illustrated by Clarke (and possibly derived from the York River Formation; P. J. Lespérance, personal commun.) more closely resemble (ironically) *P. c. canadensis*, particularly in eye morphology. However, small specimens collected from the Upper Grande Grève Formation are close to the specimens figured by Clarke, and it is herein assumed that Clarke's figured material is representative of a single taxon.

The terminal segment of the pygidial axis in

most specimens merges smoothly with the posterior pleural field (as is typical for *cristata*); this observation conflicts to some extent with some of Clarke's illustrations (1908 [1908–1909], pl. 10, figs. 5, 6). Presence of well-separated granules that do not form ridges on the cephalic doublure, rosette-like development of glabellar tuberculation, and axial furrow nodes on the internal mold of the thorax are plesiomorphic. Considering that *P. c. gaspensis* is among the older of the subspecies of *P. cristata* known, however, it is remarkable that it is relatively more advanced in some important characters (especially in the eye and morphology of the posterior region of the glabella) than some other taxa, especially *P. c. variabilis*.

RELATIONSHIPS AMONG SUBSPECIES OF *PHACOPS CRISTATA*

My interpretation of the relationships among these subspecies is summarized in figure 36. Two conspicuous pairs of sister taxa are recognized: *P. cristata canadensis*–*P. c. stummi* (with *P. c. nasutus* also closely related), and *P. c. cristata*–*P. c. bombifrons*. *Phacops cristata gaspensis* and *P. c. variabilis* are each considered relatively plesiomorphic to the other subspecies, but in themselves do not constitute a sister group.

Although all characters used in the present study were evaluated to formulate this theory of relationships, by far the more important were the number of dorsoventral files and its variability, relative number of lenses per dorsoventral file, morphology of the posterior glabellar region, general shape and inclination of the composite glabellar lobe, and ornamentation of the anterior cephalic doublure. Development of spinescence, which materially aids in the de-

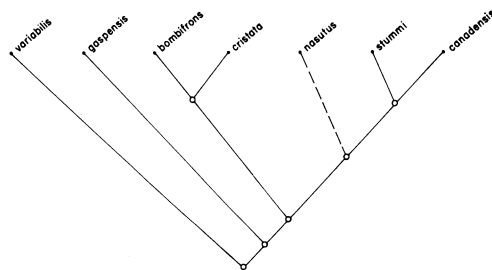


FIG. 36. Theory of relationships of subspecies of *Phacops cristata*.

lineation of the separate subspecies, is difficult to evaluate for the present purposes of elucidating relationships.

I herein consider stability in number of dorsoventral files in *P. cristata* to be derived, relative to a variable number. Stability is associated with a relatively low number of dorsoventral files (usually 14), i.e., there are no populations known to me with a stable number of dorsoventral files greater than 14. It is difficult, however, to adduce a strong argument to support the conclusion that stability in dorsoventral file number is ipso facto derived, but as populations variable in dorsoventral file number generally show that higher numbers of dorsoventral files are reached only in larger specimens, it is possible that a pedomorphic effect, resulting in a phylogenetic reduction of dorsoventral files is operative. In such a case, larger numbers of dorsoventral files would be primitive; I have elsewhere (Eldredge, 1972b) argued a similar case for dorsoventral file number distribution in subspecies of *P. rana*, although the evidence in that case was perhaps less ambiguous.

Although relative number of lenses in homologous dorsoventral files could be expected to vary as a function of adaptation to local environments, the presence of a tuberculated callosity under the visual surface in some samples with a relatively short height of the visual surface (and consequently relatively few lenses) suggests a secondary (derived) condition from a primitive, tall visual surface with many lenses. However, probably not all populations with short visual surfaces are shared apomorphs in this regard.

As argued above for *Phacops logani*, presence of a complete intercalating ring is probably primitive. It is unlikely that, once incorporated into the composite glabellar lobe, an intercalat-

ing ring would reappear in phylogeny. Also, a glabellar profile wherein the glabella is only moderately inclined anterodorsally (in standard orientation) is much more the rule in phacopid taxa as a whole than is the steep inclination, and very high anterior arch, developed in subspecies of *Phacops cristata*. Finally, and for similar reasons, a wholly granulated cephalic doublure is primitive when compared with one ornamented with granules medially, and wavy, interconnected ridges posterolaterally, or one with wavy ridges over the entire surface of the doublure.

It is mostly with these characters in mind that the theory of relationships shown in figure 36 was arrived at. *Phacops cristata variabilis*, with a variable and sometimes large number of dorsoventral files, and frequent retention of a complete intercalating ring, is considered the most plesiomorphic subspecies, and morphologically closest to the ancestor of the entire species. *Phacops cristata canadensis* and *P. c. stummi* form a highly derived sister group characterized particularly by a high angle of inclination of the composite glabellar lobe. This group is in turn a sister group of *P. c. cristata*-*P. c. bombifrons* (allied primarily by glabellar shape and profile) into a major taxon determined especially by loss of the intercalating ring (except some small *P. c. bombifrons*). *Phacops cristata gaspensis* shows, along with the foregoing taxa, a reduced number of dorsoventral files, and general absence of the intercalating ring, whereas the shared derived characters of *P. cristata variabilis* are those of the entire species. It is noteworthy that, although one of the oldest subspecies of *Phacops cristata*—*P. c. gaspensis*—is relatively plesiomorphic, *P. cristata variabilis*, the most plesiomorphic subspecies, occurs in strata coeval with and even perhaps younger (i.e., Ragland Formation) than those rocks in which all other subspecies occur.

RELATIONSHIPS AMONG NORTH AMERICAN SPECIES OF *PHACOPS*

IN MY OPINION, *Phacops logani*, *P. claviger*, *P. clarksoni*, *P. cristata*, and *P. iowensis* (see Eldredge, 1972b) form a closely knit, monophyletic taxon. This conclusion is based, not on the ready availability of one or more shared-derived characters which clearly unite the group and distinguish them from all others, but rather on the existence of morphoclines in all characters exhibiting significant interspecific variation. The more important morphoclines, and their interpreted polarities, are reviewed briefly below.

Those characters of the cephalon which exhibit the most conspicuous interspecific variation are glabellar ornamentation; glabellar shape; conformation of the posterior region of the glabella; spinescence; the number and intra-populational stability of dorsoventral files, lens and dorsoventral file dimorphism or monomorphism; ornamentation of the cephalic doublure; and shape of the hypostomal suture.

There is a distinct morphocline in glabella ornamentation from a groundmass of granules lying between and covering larger tubercles (*P. logani*, *P. claviger*) to larger tubercles with a groundmass of extremely fine granules (*P. l. clarkei*), to an absence of a granular groundmass but with larger tubercles showing traces of a "rosette" pattern (some *P. cristata gaspensis* and *P. c. stummi*) through to a pattern of large, simple tubercles, generally of different size classes (*P. clarksoni*, most *P. cristata*, *P. iowensis*). As previously discussed, there is good reason to believe that possession of a groundmass of granules is primitive for this group and that the absence of such a feature is derived.

In standard orientation, the glabella of most subspecies of *Phacops logani* and of *P. claviger* is high ("tumid" or "inflated") and in lateral aspect, the dorsal surface of the composite glabellar lobe is only slightly inclined antero-dorsally in both species. The glabella is somewhat flattened in *P. logani clarkei*, *P. l.* subspecies A, *P. clarksoni*, and *P. iowensis*, and in these taxa, the dorsal surface of the composite glabellar lobe remains relatively horizontal. The same is true of *P. cristata variabilis*; the glabella is relatively tumid in *P. c. cristata* and *P. c. bombifrons*, and relatively flat but inclined strongly anterodor-

sally in *P. c. stummi*, *P. c. nasutus*, *P. c. canadensis*, and *P. c. gaspensis*. A tumid but horizontal glabella is herein considered primitive, and a flattened one derived; a high anterodorsal slope reflects a further specialization.

A deeply incised and completely connected 1p glabellar furrow, forming a conspicuous intercalating ring with distal nodes and a median lobe which is recurved slightly anteriorly, is primitive. Such a condition is found in *P. logani logani*, *P. l. birdsongensis*, *P. l. raymondi*, *P. claviger*, some *P. clarksoni*, most *P. cristata variabilis*, and most *P. iowensis*. The key taxon here is *P. cristata variabilis*; whereas some specimens, especially from the Needmore shale of Virginia, show an almost complete loss of the intercalating ring, this structure is well developed in others. Although possession of a well-developed intercalating ring is plesiomorphic and not per se indicative of affinities, nevertheless, its presence in a major subspecies of *P. cristata* negates Maximova's (1971) concept of *Via-phacops* and affords a link between *P. iowensis* (also plesiomorphic in this respect) and *P. cristata sensu lato*. At the same time, retention of this character also helps bridge the morphological gap between specialized *P. cristata* subspecies and *Phacops logani sensu lato*.

Genal and occipital spinescence is a relatively unusual feature in holaspide phacopids, and always to be considered derived. The ability to produce such spines itself would seem to be a shared derived character which helps unite the entire group (except *P. iowensis*). However, even though such spines may have been homologous, their variable development within some populations strongly suggests they were developed independently several different times. Thus *P. cristata canadensis* shares no particularly strong relationship with *P. clarksoni* just because both possess large genal spines (and lack an occipital spine). The intrapopulational variability in spinescence also enables *P. iowensis* to be considered within the larger taxon, as there are some subspecies of *P. cristata* (particularly *P. c. variabilis*) and *P. logani* (e.g., *P. l. birdsongensis*) which also frequently, or even usually, lack spines.

In an earlier paper (1972b), I recognized a morphocline of 17 dorsoventral files in *P. logani*, 16 in "*P. hudsonicus*," 15 in "*P. raymondi*," 14 in *P. cristata*, and 13 in *P. iowensis*. The present study has revealed the gross over-simplification of such a scheme. "*Phacops hudsonicus*" is now to be considered the small-eyed variant of *P. logani logani*, and "*P. raymondi*" as a subspecies of *P. logani*. Furthermore, whereas most *P. l. logani* do in fact have 17 dorsoventral files, 18 and 19 are not too uncommon, and *P. l. raymondi* (as well as *P. l. birdsongensis*) shows a considerable range in number of dorsoventral files. This variation has been discussed above in conjunction with *P. logani*.

In general, there is almost total stability in the holospid stage in number of dorsoventral files in *P. iowensis* (13), near total stability in *P. cristata nasutus*, *P. c. cristata*, and *P. c. bombifrons* (14), and stability (as far as is known) in *P. clarksoni* (17). There is no NDV-NLNS dimorphism in these taxa, nor in *P. c. variabilis* and *P. c. gaspensis*. I consider a large number of dorsoventral files to be primitive, and a smaller number derived. (The capacity for variation in this character is so great that relationships should be established on other criteria before dorsoventral file counts are compared. However, those characters discussed above, as well as those to be considered below, show that these taxa are sufficiently closely related so the number of dorsoventral files can be compared). In short, although the details of my prior discussion (Eldredge, 1972b, p. 59) were incomplete and somewhat incorrect, I believe the basic pattern holds, and that both a reduction in dorsoventral file number, and an increase in its intrapopulational stability, occurred in the phylogeny of these species.

The loss of dimorphism is problematical, however, as there are two conflicting lines of evidence. *Phacops cristata gaspensis*, one of the earliest subspecies of *P. cristata*, has relatively few lenses per dorsoventral file and from 12–14 dorsoventral files. It is thus quite similar to the small-eyed variant of, e.g., *P. logani raymondi*. However, *P. cristata variabilis* (and, to a lesser degree, *P. c. bombifrons*) in some cases develops 15 or 16 dorsoventral files, suggesting that the reduction to 14 dorsoventral files may have involved the large-eyed *P. logani* forms. In general, the former hypothesis seems preferable, and I tentatively conclude that the develop-

ment of a monomorphic pattern, centering around 14 dorsoventral files, reflects the derived adoption of the small-eyed *logani* variant morphology. The presence of a large number of lenses in *P. cristata cristata*, then, amounts to a secondary increase in that variable.

The vincular furrow also shows significant variation among these species. From 8–11 notches have been observed, with *P. logani* tending to have fewer than *P. cristata* or *P. iowensis*. Both the distal and proximal walls are indented to form these notches in *P. logani* and most subspecies of *P. cristata*, although generally only the proximal wall is notched in *P. cristata variabilis* and *P. iowensis*. I have no idea which condition is to be regarded as primitive. The vincular furrow is quite shallow anteromedially in some subspecies of *P. logani*, in *P. claviger*, and in *P. clarksoni*, and deep and continuous in *P. cristata* and *P. iowensis*, but, here again, it is difficult to adjudge polarity, and *P. cristata* and *P. iowensis* may not, in fact, share a derived condition of the vincular furrow.

The ornamentation of the cephalic doublure provides a more convincing morphocline. Granules covering the entire surface proximal to the vincular furrow is probably a primitive condition, and is typical of the *P. logani* complex. *Phacops cristata*—with one conspicuous and important exception—retains the granules anteromedially, but develops connected granules (formed into wavy ridges) posterolaterally. The one exception, a single specimen of *P. cristata cristata*, shows terrace lines over the entire cephalic doublure. Other specimens of *P. cristata cristata*, however, retain the granules. *Phacops iowensis* shows only terrace lines. Thus, the ornament of the cephalic doublure in *P. iowensis*, so strikingly different from that of *P. logani*, is, in fact, bridged entirely by a spectrum of variation within *P. cristata*.

The shape of the hypostomal suture shows a vague morphocline from a slight posteriad convexity (some *P. logani*) through being essentially straight (some *P. logani*, most *P. cristata*, some *P. iowensis*) to being slightly concave (some *P. cristata*, most *P. iowensis*). According to Campbell (1967) this convexity (posteriad) is primitive in related taxa, and concavity derived. The variation in this character is too slight, however, to warrant any strong conclusions concerning relationships among the taxa considered in this study.

The hypostomata of *P. logani*, *P. claviger*, and *P. cristata* insofar as known are all rather similar; no hypostomata are known for *P. clarksoni* or *P. iowensis*. All the hypostomata for the three species seem to lack the posterior projection seen in, e.g., *P. rana*; in contrast to *P. rana*, the hypostomata of these three species are nearly as wide as long. The maculae are conspicuous, situated on the anterolateral region of the central body, generally detached from the marginal furrow. In all three species the hypostoma is covered with granules. Aside from the possibility that the central body is convexly rounded in *P. cristata* and relatively flatter in *P. logani* and *P. claviger*, lack of adequate material precludes the use of the hypostoma in evaluating differences between, and in assessing relationships among, these species.

Besides the presence of nodes in the axial furrows (some *P. logani*) and their absence (except on external molds) in other taxa, and the reduction of the "Panderian" notches in some *P. cristata* and *P. iowensis*, the thorax reveals relatively little of interest in terms of relationships. Axial nodes and spines are, of course, derived, but their presence or absence cannot be taken as a straightforward indication of close affinity among these species.

It is difficult to differentiate isolated pygidia of *P. logani* and *P. cristata*. Although some slight differences in proportion undoubtedly exist, the main difference seems to be that the terminal piece of the axis is bluntly rounded posteriorly in *P. logani*, whereas it merges more gradually with the posterior pleural field in *P. cristata*. The presence of up to five interpleural furrows on *P. iowensis* (Eldredge, 1972b) is of importance, however, as interpleural furrows are generally poorly developed on species of *Phacops* in Campbell's (1967) restricted definition of that genus.

When all these characters are taken into

consideration, some conflicts in morphocline polarity—hence recognition of sister taxa—are apparent, but the overwhelming indication is that the species are related in the manner shown in figure 37. *Phacops iowensis* and *P. cristata* are sister species; *P. iowensis* is apomorphic in terms of NDV and cephalic doublure morphology. It is, however, plesiomorphic in glabellar profile, conformation of the posterior region of the glabella, and in lack of spines. Characters that I consider shared-derived which tie these two species together are the monomorphic and overall close similarity of the pattern of eye morphology and glabellar (and to a limited extent, cephalic doublure) ornamentation.

Phacops claviger and *P. logani* are also closely related, as discussed previously. It is true, however, that most of their shared characters are here adjudged to be primitive, or, if derived, not significant (e.g., spinescence). Thus, within this matrix of two pairs of sister species, *P. clarksoni* looms as an intermediate; it is plesiomorphic, especially with respect to the vincular furrow and eye morphology, and thus closely resembles some *P. logani* (especially *P. logani clarkei*). But glabellar ornamentation and the advanced position of the intercalating ring are derived features shared with *P. cristata* and *P. iowensis*. I therefore consider it a sister taxon with *P. cristata*-*P. iowensis*, and all three species form a sister group with *P. logani*-*P. claviger*.

No attempt has been made in the present study to reflect these relationships in a revised classification. It is clear, however, that separate generic status could be accorded the *P. logani*-*P. claviger* group and the *P. clarksoni*-*P. cristata*-*P. iowensis* group. Furthermore, other taxa undoubtedly occur elsewhere [as indeed Maximova (1971) has claimed], that are closely allied with these two separate groups. The problem, however, lies with *P. iowensis*, as (1) it is clearly closely related to *P. cristata*, but (2) its morphological "grade" is similar to that of other taxa—e.g., *Phacops rana*—with which it is not especially closely related (Eldredge, 1972b), but which Campbell (1967) considered diagnostic of *Phacops sensu stricto*. However, it would be difficult to write a restricted diagnosis of *Phacops* omitting *P. iowensis*. Clearly, the phylogenetic relationships of all known Devonian phacopid species must be studied before any attempt is made to reclassify this interesting group.

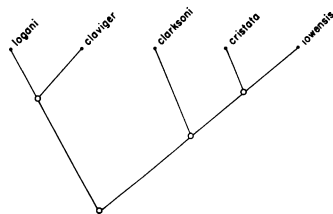


FIG. 37. Theory of relationships of five Devonian species of *Phacops*.

APPENDIX

LOCALITY LIST

THE AMERICAN MUSEUM OF NATURAL HISTORY

Phacops logani

- 3086. Ross limestone. North side of Rt. 64, at Olive Hill, Tennessee.
- 3087. Birdsong shale. East side of Rt. 69, 9.5 miles north of Parsons, Tennessee.
- 3088. Birdsong shale. 3.7 miles north of intersection of Rts. 100 and 13, on Rt. 13, near Linden, Tennessee.
- 3089. Kalkberg and New Scotland formations. Along access road between Thruway exit 21 and Rt. 23, vicinity of Catskill, New York.
- 3090. Kalkberg and New Scotland formations. Roadcut near Thruway underpass, approximately 0.5 mile west of Broncks Lake, Cocksackie Quadrangle, New York.
- 3091. Kalkberg and New Scotland formations. Dann's Hill, 1.1 miles northeast of intersection of Bridge and Sunnyside roads, on Sunnyside Road, north of Schoharie, New York.
- 3092. Kalkberg Formation. Along U. S. Rt. 20 at Cherry Valley, New York.
- 3093. New Scotland Formation. Entrance to John Boyd Thacher State Park, New York.
- 3094. Glenerie Formation. Quarry of the Universal Atlas Cement Co. at Becraft Mountain, Hudson, New York.
- 3095. Murailles and Mont Joli formations. At Percé, Gaspé Peninsula, Quebec.
- 3096. Roncelles Formation. Along Rte. 6, near Cap-des-Rosiers, Gaspé Peninsula, Forillon, Quebec.
- 3097. Roncelles Formation. East of Anse-aux-Griffon, Gaspé Peninsula, Quebec.
- A. Haragan Formation. Various unidentified Oklahoma localities.

Phacops logani in the James Hall Collection of the American Museum of Natural History cannot be satisfactorily localized. All specimens are listed as "Lower Helderberg Group" and most come from the Helderberg vicinity near Albany, New York, from the Kalkberg-New Scotland interval. The holotype of "*P. hudsonicus*," however, comes from the Kalkberg or New Scotland formations at Becraft Mountain, Hudson, New York.

Phacops clarksoni

All seven known specimens of *P. clarksoni* appear to come from the Schoharie Formation somewhere in the Schoharie Valley in New York. All are in the James Hall Collection.

Phacops cristata

- 3098. Needmore Formation. South side of Rt. 522 at Gainsboro, Virginia.
- 3099. Needmore Formation, Intersection of Rt. 600 and U.S. Rt. 50 at Hayfield, Virginia.
- 3100. Schoharie Formation. In woods along Rt. 85, approximately 0.5 mile north of intersection with Rt. 43, near Clarksville, New York.
- 3101. Schoharie Formation. In woods near Calanan's Corners, west of South Bethlehem, New York.
- 3102. Buttermilk Falls Formation. East side of Rt. 209, just north of East Stroudsburg, Pennsylvania.
- 3103. Onondaga Formation. Exposures along Rt. 20 at Cherry Valley, New York.
- 3104. Esopus Formation. Along railroad tracks at Highland Mills, New York.
- 3105. Grande Grève Formation. Exposures along Rte. 6, Gaspé Peninsula (Forillon), Quebec.

Many specimens of *Phacops cristata* from the Schoharie and Onondaga formations of New York are in the James Hall Collection of the American Museum of Natural History. The localities are not sufficiently precise to warrant listing herein. A few specimens from the Columbus limestone of Ohio and the "Onondaga" limestone of Ontario are also included in the collection.

In the G. K. Greene Collection of the American Museum of Natural History, there is the following:

- 3106. Jeffersonville Formation. Falls of the Ohio River at Jeffersonville, Indiana.

NEW YORK STATE MUSEUM

Material from the collections of the New York State Museum utilized in this study involved type and figured specimens of Hall (1861a, 1861b, 1862, 1876), Hall and Clarke (1888) and Clarke (1908). *Phacops logani* material is listed as coming from "New Scotland beds, Schoharie, New York," probably almost the same locality as AMNH loc. 3091. Schoharie Formation material comes largely from the Schoharie and Clarksville regions of New York, whereas Onondaga Formation material comes from Canandaigua, Leroy, Lime Rock, and Clarence, New York and from Walpole and North Cayuga, Ontario. Clarke's (1908) material is from the Grande Grève and possibly the York River formations, near Grande Grève, Gaspé Peninsula, Quebec.

UNIVERSITÉ DE MONTRÉAL

1. Quay Rock Member, Cap Bon Ami Formation. From the Forillon, Gaspé Peninsula, Quebec.
2. Upper Grande Grève Formation. Same as AMNH loc. 3105.

UNIVERSITY OF MICHIGAN

1. Haragan Formation. 3 miles northeast of Crusher, Oklahoma.
2. Bailey limestone. Hill south of Ozora, Little Saline Creek, Missouri.
3. Little Saline limestone. Little Saline Creek, Ste. Genevieve Co., Missouri.
4. "Lower Onondaga limestone." Port Colborne, Ontario.
5. Columbus limestone. Abandoned Wagner Quarry, 1.5 miles southwest of Castalia, Erie County, Ohio.
6. Bois Blanc Formation. West side of McGulpin Point, sec. 10, T. 39N, R. 4W, 2.5 miles west of center of Mackinaw City, Michigan.
7. Amherstburg Formation. Abandoned Cummins Quarry, south side of Halfway Creek, S. 1/2 sec. 2, T. 8S, R. 6E, 6 miles south and 1.75 miles east of Petersburg, Monroe County, Michigan.
8. Jeffersonville Formation. Same as AMNH loc. 3106.

NATIONAL MUSEUM OF NATURAL HISTORY

1. "Becraft Formation." 1 mile south of Newcastle, Virginia.
2. Haragan Formation. Coal Creek, NW 1/4 SE 1/4, NW1/4 22-IN-7E, Pontotoc County, Oklahoma.
3. Haragan Formation. White Mound vicinity, 3 miles west of Nebo, Murray County, Oklahoma.
4. Haragan Formation. (USNM loc. 483d). West facing scarp, SW 1/4-NW 1/4, 8-18-8E, near old Hunton, Coal County, Oklahoma.
5. Haragan Formation. Hunton townsite, west of Clarita, Oklahoma.
6. Haragan Formation. Atoka Quadrangle, SW corner sec. 16, T1S, R8E, Oklahoma.
7. Ragland Formation. (USNM loc. 538v). Abandoned quarry 1.5 miles south-southeast of Ragland, Springville Quadrangle, Alabama.
8. Needmore Formation. Blair County, Pennsylvania.

VANDERBILT UNIVERSITY

1. Birdsong Formation. Williams Mill, Tennessee.
2. Birdsong Formation. At Big Sandy, Tennessee.

YALE PEABODY MUSEUM

1. Birdsong Formation. Swayne's Mill, Henry County, Tennessee.

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