RECENT DEVELOPMENTS IN THE PALEOBIOLOGY OF TRILOBITES

LOREN E. BABCOCK

Kansas Geological Survey
and
The University of Kansas

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Loren E. Babcock

These notes provide a very brief synopsis of the proposed short course, a relatively limited number of references, some associated questions that might act as points for discussion, and some illustrations from my unpublished research. With only two lengthy lectures, I can only provide some highlights of recent research on trilobites. The information presented includes some that seems to be important today and offers potentially greater promise through the next decade or two. Topics stressed are those that should be most relevant to paleontologists studying other groups of invertebrates, stratigraphers, and other geoscientists.

There is obviously no textbook that serves the needs of this short course. Much of the material that I will present is new, and based on my unpublished research. I have listed below some readings from the English-language literature that will help to provide some background, and that will help to show the importance of fossils in general, and trilobites in particular, for solving larger geological or evolutionary problems.

GOALS OF THE SHORT COURSE:

1. To introduce some basic trilobite paleobiology

2. To learn why understanding trilobite paleobiology is important for solving other geological problems

3. To pose questions questions concerning significant new lines of research that have important implications for other disciplines of the geological and biological sciences

TOPICS TO BE COVERED:

1. Introduction to trilobite paleobiology

2. Phylogenetic analysis (numerical cladistics)

3. Heterochrony

4. Malformations

5. Biogeography

SUGGESTED READING LIST

1. INTRODUCTION TO TRILOBITE PALEOBIOLOGY

Briggs, D. E. G., and Fortey, R. A. 1989. The early radiation and relationships of the major arthropod groups. Science 246:241-243.

Cisne, J. L. 1974. Trilobites and the origin of arthropods. Science 186: 13-18.

Müller, K. J., and Walossek, D. 1987. Morphology, ontogeny, and life habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden. Fossils and Strata 19, 124 p. [Skim; read p. 52-54.]

Robison, R. A. 1987. Superclass Trilobitomorpha, p. 221-241. In: Boardman, R. S., Cheetham, A. H., and Rowell, A. J., Fossil Invertebrates. Blackwell Scientific Publications, Palo Alto, California.

Robison, R. A., and Kaesler, R. L. 1987. Phylum Arthropoda, p. 205-221. In: Boardman, R. S., Cheetham, A. H., and Rowell, A. J., Fossil Invertebrates. Blackwell Scientific Publications.

Whittington, H. B. 1977. The Middle Cambrian trilobite *Naraoia*, Burgess shale, British Columbia. Philosophical Transactions of the Royal Society of London 280: 409-443. [Skim only.]

2. PHYLOGENETIC ANALYSIS (NUMERICAL CLADISTICS)

Ashlock, P. D. 1987. Classification: philosophies and methods, p. 42-51. In: Boardman, R. S., Cheetham, A. H., and Rowell, A. J., Fossil Invertebrates. Blackwell Scientific Publications.

Cracraft, J. 1983. Cladistic analysis and vicariance biogeography. American Scientist 71: 273-281.

Fink, W. L. 1988. Phylogenetic analysis and the detection of ontogenetic patterns, p. 71- 91. In: McKinney, M. L. (ed.), Heterochrony in Evolution: a Multidisciplinary Approach. Plenum Press, New York.

Jell, P. A. 1975. Australian Middle Cambrian eodiscoids with a review of the superfamily. Palaeontographica A, 150: 1-97. [See p. 11-25.]

Wiley, E. O. 1981. Phylogenetics: the Theory and Practice of Phylogenetic Systematics. John Wiley & Sons, New York. [Skim only.]

3. HETEROCHRONY

Gould, S. J. 1988. The uses of heterochrony, p. 1-13. In: McKinney, M. L. (ed.), Heterochrony in Evolution: a Multidisciplinary Approach. Plenum Press, New York.

McKinney, M. L. 1988. Classifying heterochrony: allometry, size, and time, p. 17-34. In: McKinney, M. L. (ed.), Heterochrony in Evolution: a Multidisciplinary Approach. Plenum Press, New York.

McNamara, K. J. 1981. Paedomorphosis in Middle Cambrian xystridurine trilobites from northern Australia. Alcheringa 5: 209-224.

McNamara, K. J. 1986. A guide to the nomenclature of heterochrony. Journal of Paleontology 60: 4-13.

McNamara, K. J. 1986. The role of heterochrony in the evolution of Cambrian trilobites. Biological Reviews 61: 121-156.

McNamara, K. J. 1988. The abundance of heterochrony in the fossil record, p. 287-325. In: McKinney, M. L. (ed.), Heterochrony in Evolution: a Multidisciplinary Approach. Plenum Press, New York.

Müller, K. J., and Walossek, D. 1987. Morphology, ontogeny, and life habit of Agnostus pisiformis from the Upper Cambrian of Sweden. Fossils and Strata 19, 124 p. [See p. 52-54.]

Robison, R. A. 1967. Ontogeny of Bathyuriscus fimbriatus and its bearing on affinities of corynexochid trilobites. Journal of Paleontology 41: 213-221. [Skim only.]

Robison, R. A., and Campbell, D. P. 1974. A Cambrian corynexochid trilobite with only two thoracic segments. Lethaia 7: 273-282. [Skim only.]

Tissot, B. N. 1988. Multivariate analysis, p. 35-51. In: McKinney, M. L. (ed.), Heterochrony in Evolution: a Multidisciplinary Approach. Plenum Press, New York.

4. MALFORMATIONS

Babcock, L. E., and Robison, R. A. 1989. Preferences of Palaeozoic trilobites. Nature 337: 695-696. [Also see comments by D. P. Maitland and S. Stigler, Nature 339: 105-106 (1989).]

Babcock, L. E., and Robison, R. A. 1989. Asymmetry of predation on trilobites. 28th International Geological Congress (Washington, D.C.) 1: 66.

Bradshaw, J. L. 1988. The evolution of human lateral asymmetries: new evidence and second thoughts. Journal of Human Evolution 17: 615-637. [Skim only.]

Briggs, D. E. G., and Whittington, H. B. 1985. Terror of the trilobites. Natural History 94(12): 34-39.

Bermúdez de Castro, J., Bromage, T. G., and Fernández Jalvo, Y. 1988. Buccal striations on fossil human anterior teeth: evidence of handedness in the middle and early Upper Pleistocene. Journal of Human Evolution 17: 403-412. [Skim only.]

Conway Morris, S., and Jenkins, R. J. F. 1985. Healed injuries in Early Cambrian trilobites from South Australia. Alcheringa 9: 167-177.

McMenamin, M. A. S. 1987. The emergence of animals. Scientific American 255(4): 94-102.

Owen, A. W. 1985. Trilobite abnormalities. Transactions of the Royal Society of Edinburgh 76: 255-272.

Signor, P. W. III, and Brett, C. E. 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution. Paleobiology 10: 229-245.

Toth, N. 1985. Archaeological evidence for preferential right-handedness in the Lower and Middle Pleistocene, and its possible implications. Journal of Human Evolution 14: 607-614. [Skim only.]

Whittington, H. B., and Briggs, D. E. G. 1985. The largest Cambrian animal, <u>Anomalocaris</u>, Burgess shale, British Columbia. Philosophical Transactions of the Royal Society of London B 309: 560-609. [See p. 599-602.]

5. BIOGEOGRAPHY

Archer, A. W., and Maples, C. G. 1987. Monte Carlo simulation of selected binomial similarity coefficients (I): effect of number of variables. Palaios 2: 609-617.

Conway Morris, S. & Rushton, A. W. A. 1988. Precambrian to Tremadoc biotas in the Caledonides, p. 93-109. In: Harris, A. L. & Fettes, D. J. (eds.), The Caledonian-Appalachian Orogen. Geological Society Special Publication 38.

Cook, H. E., and Taylor, M. E. 1975. Early Paleozoic continental margin sedimentation, trilobite biofacies, and the thermocline, western United States. Geology 3: 559-562.

Fortey, R. A. 1985. Pelagic trilobites as an example of deducing the life habits of extinct arthropods. Transactions of the Royal Society of Edinburgh 76: 219-230. [Skim only.]

Fortey, R. A., and Cocks, L. R. M. 1986. Marginal faunal belts and their structural implications, with examples from the Lower Palaeozoic. Journal of the Geological Society, London 143: 151-160. [Skim only.]

Hazel, J. E. 1977. Use of certain multivariate and other techniques in assemblage zonal biostratigraphy: examples utilizing Cambrian, Cretaceous, and Tertiary benthic invertebrates, p. 187-212. In: Kauffman, E. G., and Hazel, J. E. (eds.), Concepts and Methods of Biostratigraphy. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania.

Jell, P. A. 1974. Faunal provinces and possible planetary reconstruction of the Middle Cambrian. Journal of Geology 82: 319-350.

Lipps, J. H., and Hickman, C. S. 1982. Origin, age, and evolution of Antarctic and deep-sea faunas, p. 325-356. In: Ernst, W. G., and Morin, J. G. (eds.), The Environment of the Deep Sea. Rubey Volume II. Prentice-Hall, Englewood Cliffs, New Jersey. [See p. 334-344.]

Palmer, A. R. 1972. Problems of Cambrian biogeography. International Geological Congress, 24th Session (Montreal), Section 7: 310-315.

Rowell, A. J., McBride, D. J., and Palmer, A. R. 1973. Quantitative study of Trempealeauian (latest Cambrian) trilobite distributions in North America. Geological Society of America, Bulletin 84: 3429-3442.

Secor, D. T., Jr., Samson, S. L., Snoke, A. W., and Palmer, A. R. 1983. Confirmation of the Carolina slate belt as an exotic terrane. Science 221: 649-651.

Talent, J. A. The peripatetic fossils: part 5. Nature 343: 405-406.

Taylor, M. E. & Forester, R. M. 1979. Distributional model for marine isopod crustaceans and its bearing on early Paleozoic paleozoogeography and continental drift. Geological Society of America, Bulletin 90: 405-413.

Theokritoff, G. 1979. Early Cambrian provincialism and biogeographic boundaries in the North Atlantic region. Lethaia 12: 281-295.

Waterhouse, J. B. 1990. The peripatetic fossils: part 4. Nature 343: 305-308.

Williams, H., and Hatcher, R. D., Jr. 1982. Suspect terranes and accretionary history of the Appalachian orogen. Geology 10: 530-536. [Skim only.]

INTRODUCTION TO TRILOBITE PALEOBIOLOGY

BACKGROUND

1. Arthropods, exclusively marine, extinct

2. Exoskeleton composed of chitin and low-Mg calcite (almost all species)

   a. Ecdysis

   b. Protection, muscle attachment surface, gaseous exchange

3. Rich fossil record

4. Primary divisions of body: cephalon, thorax, pygidium, axial lobe, pleural lobes

5. Appendages: 4 preoral pairs, variable number of postoral pairs, biramous except for antennae (and cercae)

6. Primary groups: polymeroids, agnostoids, soft-bodied taxa

7. Stratigraphic range: Lower Cambrian to Upper Permian

   a. Major extinctions events: Late Cambrian (biomeres), Late Ordovician, Late Devonian, Late Permian

ARE THEY REALLY WELL KNOWN?

1. *Isotelus*, Ohio's State Fossil

2. By 1989, approximately 4,000 genera and 20,000 species had been described

   a. Perhaps only 1 to 5% of trilobites preserved as fossils

   b. Cambrian taxa have been underdescribed compared to those of the post-Cambrian

   c. *Isotelus* and *Phacops* are not 'typical' trilobites

3. Soft parts: well known from less than 10 species

   a. Not known from any 'typical' trilobite

4. Our concepts about diversity patterns, onshore-offshore patterns, usefulness as biostratigraphic or paleoenvironmental tools, and many other things will change dramatically in the next several decades

WHY ARE TRILOBITES IMPORTANT TO GEOLOGISTS?

1. Biostratigraphy, especially Cambrian to Ordovician, Upper Silurian to Lower Devonian

2. Paleoenvironmental analysis
3. Biogeography and plate tectonic reconstructions
4. Evolutionary patterns, including putuated equilibrium, phyletic gradualism, macroevolution, heterochrony
5. Extinction events
6. Structural analyses of strain in orogenic belts
7. Isotopic analyses (chemistry of ancient seawater)
8. Morphometrics

PHYLOGENETIC ANALYSIS (NUMERICAL CLADISTICS)

BACKGROUND

1. Semi-quantitative method for analyzing phylogenetic relationships

   a. Similarities in characters are apportioned on a branching diagram according to the hierarchical level at which they characterize groups

   b. Characters, transformation states

   c. Transformation states polarized using either the ontogenetic criterion or the outgroup criterion

   d. Computer programs: PAUP, Hennig86, MacClade

IMPORTANCE AND MAJOR CONTRIBUTIONS:

1. Explicit method of reconstructing evolutionary patterns

2. Permits easy recognition of important evolutionary novelties

3. Permits easy recognition of convergences and parallelisms

4. Can aid in developing a classification of organisms that reflects evolutionary history

TERMINOLOGY

CHARACTER: A comparative unit present in an organism

CHARACTER STATE: Specific expression of a character in an individual taxon

TRANSFORMATION SERIES: A group of homologous characters

POLARITY: Ordering of characters into plesiomorphous and apomorphous states

APOMORPHY: Derived character

SYNAPOMORPHY: Shared derived character

AUTAPOMOROHY: Unique derived character

PLESIOMORPHY: Primitive character

SYMPLESIOMORPHY: Shared primitive character

HOMOPLASY: includes convergence (development of two similar characters from different preexisting characters) and parallelism (development of similar characters independently from the same ancestral character)

INGROUP: The group of study taxa

OUTGROUP: A group of organisms that is related to but removed from the group of study taxa (geneologically most closely related to the ingroup)

SISTER GROUP: The group of organisms most closely related to the study taxa (excluding their direct descendants)

MONOPHYLETIC GROUP (CLADE): A group of species that includes an ancestral species and all of its descendants

PARAPHYLETIC GROUP: An artificial group in which one or more descendants of an ancestor are excluded from the group

POLYPHYLETIC GROUP: An artificial group in which the common ancestor is placed in another taxon

CLADOGENESIS: The branching component of phylogeny

ANAGENESIS: The relative amount of morphological or genetic change between speciation events

IS IT POSSIBLE TO RELIABLY RECOVER PHYLOGENETIC RELATIONSHIPS FROM FOSSIL ORGANISMS?

1. Several distinguished neontologists have said "no"

2. Much information, especially about soft parts, has been lost

3. There is a tendency to use the time of appearance in geological history as a criterion for polarizing characters

CAN WE TEST THE RELIABILITY OF PHYLOGENETIC PATTERNS DERIVED FROM ANALYSES OF HARD PARTS?

1. No direct test for trilobites

2. Can test closely related groups that have living representatives (taxonomic uniformitarianistic approach)

   a. Test using the major groups of ostracodes

PHYLOGENETIC RELATIONSHIPS AMONG THE MAJOR GROUPS OF TRILOBITES

1. Importance:

   a. Relationships of the major groups have not been worked out (but classification systems are numerous)

   b. We need a framework within which to begin analyzing relationships of smaller groups

   c. Problem of the eodiscids: Where do they fit in relative to the polymeroids and agnostoids?

2. Data and analysis

3. Results

PHYLOGENETIC RELATIONSHIPS OF PARADOXIDIDS

1. Importance:

    a. Important biostratigraphic tools for the Middle Cambrian

    b. Relationships have been considered contentious

    c. Good group for studying heterochronic patterns

2. Data and analysis

3. Results

RELATIONSHIPS AMONG LATE PALEOZOIC TRILOBITES OF NORTH AMERICA

1. Importance:

    a. Biostratigraphy

    b. Paleoenvironmental analysis

    c. Survivors of the Frasnian-Famennian extinction event: Why was there no subsequent adaptive radiation of the kind that occurred after all other major extinctions?

    d. Why do most species and genera differ so little morphologically? Are differences among taxa related more to cladogenesis, anagenesis, or differences of taxonomic philosophy?

2. Data and analysis

3. Results

HETEROCHRONY

HISTORY

1. Relationship to biogenetic law of Haekel
2. Recent surge of interest partially because it addresses internal and external factors of evolution
3. Important authors: Gould, McNamara, Alberch, McKinney

IMPORTANCE:

1. Fast emerging as one of the most powerful tools for explaining evolutionary change in organisms
2. Easily quantifiable
3. Relationship to biostratigraphy

BASIC CONCEPTS

1. Components: time, size, shape
2. Paedomorphosis
    a. Progenesis
    b. Neoteny
    c. Post-displacement
3. Peramorphosis
    a. Hypermorphosis
    b. Acceleration
    c. Pre-displacement

HOW DOES HETEROCHRONY WORK IN TRILOBITES?

1. Ontogeny
    a. How can ontogenetic age be determined?
    b. Allometric heterochrony
2. Paedomorphosis
    a. Paedomorphoclines
3. Peramorphosis
    a. Peramorphoclines

4. Is there a difference in dominant heterochronic expression between Cambrian and post-Cambrian trilobites?

5. Are our present models of heterochrony oversimplified?

   a. Bivariate vs. multivariate techniques of analysis

   b. Example of the conocoryphid trilobites

HETEROCHRONY IN SOME IMPORTANT GROUPS OF TRILOBITES

1. Eodiscids

2. Paradoxidids

3. Late Paleozoic trilobites of North America

MALFORMATIONS

IMPORTANCE:

1. A source of much paleobiological information, although commonly overlooked or ignored

   a. Information about predator-prey interactions (identity of predator, behavior)

   b. Wound repair: phylogenetic implications

   c. Genetic variability in populations: implications for evolutionary mode (gradualism or punctuated equilibrium)

WHAT ARE THE TYPES OF MALFORMATIONS?

1. Teratologies

2. Pathological conditions

3. Injuries

HEALED INJURIES OF TRILOBITES

1. Recognition

2. Sources of injury

   a. Accidents

   b. Predation

3. Statistical analysis of predation scars of trilobites

   a. Distribution of injuries

   b. Possible relationship to handedness

   c. Evolutionary implications

BIOGEOGRAPHY

IMPORTANCE:

1. Biostratigraphy

   a. Restricted distributions vs. worldwide distributions of taxa

2. Reconstructions of oceanic and continental configurations

   a. Distance of separation between continental blocks

   b. Identification of continental margins

   c. Reconstruction of water masses in ancient oceans

3. Reconstructions of paleoenvironments

   a. Deep vs. shallow water

   b. Warm vs. cool water

   c. Restricted vs. unrestricted access to open ocean

   d. Identification of conditions of deposition of Lagerstatten

4. Relationship to extinction events

   a. Cambrian biomeres: Do they represent shifts in biofacies rather than true extinctions?

5. Controversy over Viswa Jit Gupta's fossils from the Himalaya Mountains

HISTORICAL BACKGROUND

1. Reconstructing land and sea relations has had a long history in geology

2. Important examples of the use of trilobites:

   a. Malvinokaffric Province and the reconstruction of Gondwana

   b. Acado-Baltic (Atlantic) and North American (Pacific) provinces and the history of Iapetus

   c. Quantification of biogeographic analysis

ASSUMPTIONS OF BIOGEOGRAPHIC STUDIES

1. Restriction of faunas to shallow shelf seas of single tectonic blocks

2. Deep and wide oceans inhibited faunal dispersal

3. Faunal dissimilarity between regions is a function of past geographic proximity

ARE THE ASSUMPTIONS VALID? ARE THEY TESTABLE?

1. Cluster analyses of present-day isopod distributions: comparison to trilobites

    a. Relationship between warm- and cool-water faunas

2. Multivariate analyses of North American and Acado-Baltic trilobites

PALEOCEANOGRAPHIC IMPLICATIONS

1. Were world oceans thermally stratified during parts of the Paleozoic?

2. What is the relationship of faunal distribution to paleolatitude?

3. Is there any relationship between faunal distribution and paleolongitude?

4. What is the relationship of faunal distribution to water depth?

5. How do biogeographic patterns affect interpretations of tectonic plate distributions during the Paleozoic?

    a. Small tectonostratigraphic terranes (native terranes, suspect terranes, accreted terranes)

    b. Larger tectonic blocks

6. Can we extract information about paleoceanography from a better understanding of trilobite form, function, ecology, and evolution?

    a. Identification of continental slope deposits using multivariate analyses of trilobite distributions

    b. Possibility of determining structural shortening in orogenic zones

    c. Determination of isolation events using vicariance biogeography

    d. Possible usefulness of onshore-offshore diversity trends

    e. Possible usefulness of major morphological trends (e.g., eye-bearing vs. blind species, benthic vs. pelagic species)

1) Maximum holaspid size: greater than 1 cm (0) or less than 1 cm (1).
2) Facial sutures: absent (0) or present (1).
3) Number of thoracic segments: equal to or greater than 5 (0), 3 (1), 2 (2), or 0 (3).
4) Shape of labrum: platelike (0) or saddlelike (1).
5) Pleural region of pygidium: segmented (0) or unsegmented (1).
6) Eyes: present (0) or absent (1).
7) Basal lobes: absent (0) or present (1).
8) Glabella: short and tapered (0), long and anteriorly expanded (1), short and anteriorly expanded (2), long and tapered (3), or long and bulbous anteriorly (4).
9) Cephalothoracic hinge: overlapping (0) or edge-to-edge (1).
10) Glabellar segmentation: multiple lateral furrows (0) or single transglabellar furrow (1).
11) Segmentation in pygidial axis: fully segmented (0), 3 segments in anteroaxis (1), or 2 segments in anteroaxis (2).
12) Median node or ridge on anteroaxis of pygidium: absent (0) or present (1).
13) Pleural tips of last thoracic segment: posteriorly directed (0) or anteriorly directed (1).
14) Median nodes or ridges on all thoracic segments: absent (0) or present (1).
15) Median node or ridge on posteroglabella: absent (0) or present (1).
16) Posteroaxis of pygidium: tapered (0) or expanded (1).
17) Eye ridges: present (0), absent (1), or developed into prominent palpebral-ocular ridge (2).
18) Axial width relative to pleurae: narrow (0) or wide (1).
19) Calcified exoskeleton: absent (0) or present (1).
20) Terrace lines on border: present (0) or absent (1).
21) Long axial spines in thorax: absent (0) or present (1).
22) Pleural spines in thorax: short (0) or long (1).

Figure 1. Character transformations used in a phylogenetic analysis of the major groups of trilobites. Character states correspond to adult morphology.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	EODISCUS	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
2	PAGETIA	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
3	SERRODISCUS	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
4	DAWSONIA	1	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
5	NEOCOBBOLDIA	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
6	CALODISCUS	1	0	?	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
7	TANNUDISCUS	1	1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0
8	PERONOPSIS	1	0	2	1	1	1	1	0	1	1	2	1	1	0	1	0	1	1	1	1	0	0
9	PTYCHAGNOSTUS	1	0	2	1	1	1	1	0	1	1	2	1	1	0	1	0	1	1	1	1	0	0
10	AGNOSTUS	1	0	2	1	1	1	1	0	1	1	2	0	1	0	0	0	1	1	1	1	0	0
11	ONYMAGNOSTUS	1	0	2	1	1	1	1	0	1	1	2	1	1	0	1	0	1	1	1	1	0	0
12	DIPLAGNOSTUS	1	0	2	1	1	1	1	0	1	1	2	1	1	0	1	0	1	1	1	1	0	0
13	TOMAGNOSTUS	1	0	2	1	1	1	1	0	1	1	2	1	1	0	1	0	1	1	1	1	0	0
14	CONDYLOPYGE	1	0	2	?	0	1	0	2	?	0	1	1	0	1	1	1	1	1	1	0	0	0
15	THORACOCARE	1	1	2	?	0	?	0	1	0	0	0	0	0	0	0	0	1	1	1	?	0	0
16	OLENELLUS	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	2	1	0	1	1
17	ELRATHIA	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
18	MODOCIA	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
19	OLENOIDES	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
20	MATANIA	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0
21	TONKINELLA	0	1	0	?	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	?	0	0
22	COSTADISCUS	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
23	PAGETIDES	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
24	PLEUROCTENIUM	1	0	2	?	0	1	0	2	?	0	1	1	0	1	1	1	1	1	1	?	0	0
25	XYSTRIDURA	0	1	0	0	0	0	0	4	0	0	0	0	0	0	0	0	2	0	0	0	0	1
26	NARAOIA	0	0	3	?	1	1	0	3	0	0	0	0	0	0	0	0	1	0	0	1	0	0

Figure 2. Data matrix of character states used in a phylogenetic analysis of the major groups of trilobites.

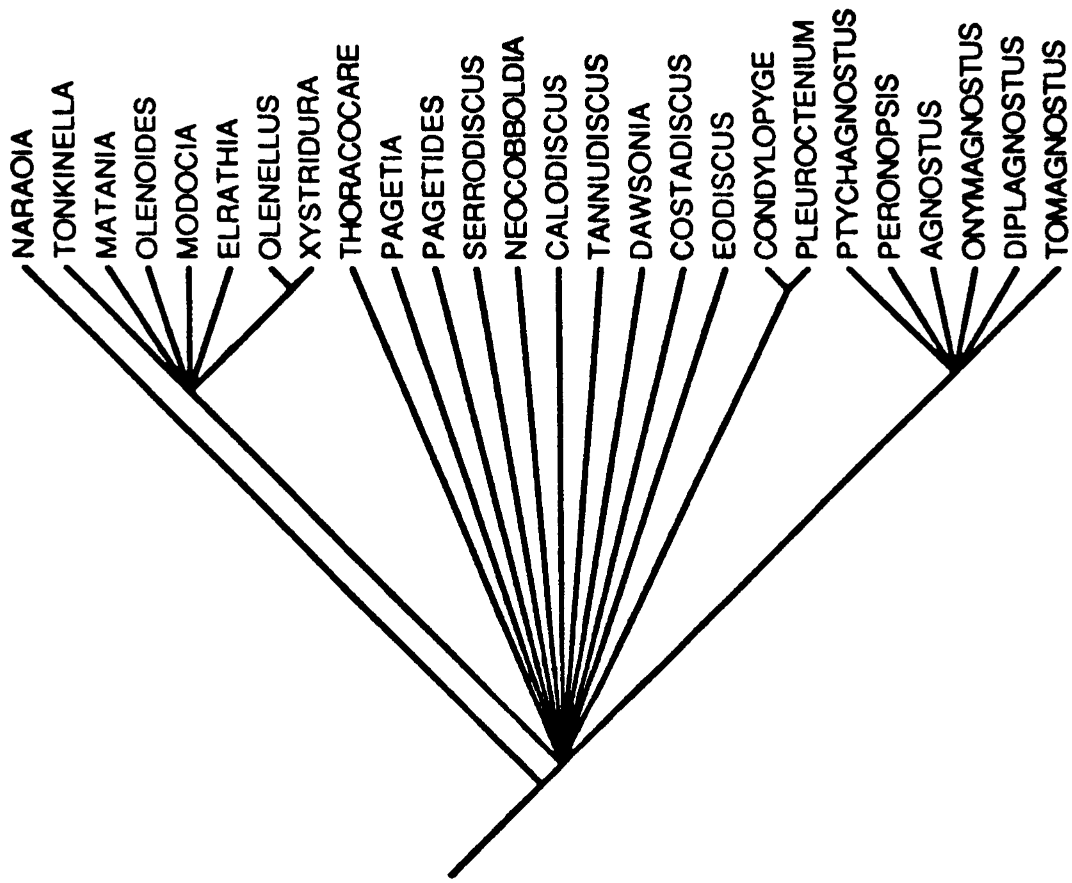


Figure 3. Strict consensus tree recovered in a phylogenetic analysis of the major groups of trilobites.

1) Anterior glabella: not expanded (0), slightly expanded (1), or greatly expanded (2).
2) Transcurrent posterior glabellar furrow: absent (0) or present (1).
3) Number of lateral glabellar furrows: 4 (0), 3 (1), 2 (2), or 0 (3).
4) Anterior glabellar furrow: transverse (0) or longitudinal (1).
5) Anterior branch of facial suture: divergent (0) or retrodivergent (1).
6) Size of pygidium: small (0), micropygous (1), or macropygous (2).
7) Number of pleural lobes in pygidium: greater than or equal to 3 (0) or less than 3 (1).
8) Number of thoracic segments: less than or equal to 13 (0), 14 to 15 (1), 16 (2), or 17-21 (3).
9) Size of rostral plate: medium (0), large (1) or small (2).
10) Anterolateral spines on labrum: absent (0) or present (1).
11) Pygidial border: present (0) or absent (1).
12) Curvature of palpebral lobes: even (0) or uneven (1).
13) Length of palpebral lobes: short (0), moderately long (1), very long (2), or to rear of cranidium (3).
14) Metafixigenal spines: absent (0) or present (1).
15) Macropleural segment in anterior thorax: absent (0) or present (1).
16) Width of pleurae: wide (0), moderately reduced (1), or much reduced (2).
17) Macropleural segments in posterior region: absent (0), ankylosed to pygidium (1), or shed into thorax (2).
18) Eye ridges: present (0) or absent (1).
19) Length of genal spines: less than or equal to one-half of body length (0) or greater than one-half of body length (1).
20) Pleural lobes: convex (0) or flat (1).
21) Axial spine in thorax: absent (0) or present (1).
22) Preoccipital ridge: absent (0) or present (1).
23) Medial nodes on pygidial axis: absent (0) or present (1).
24) Maximum holaspid size: less than 7 cm (0) or equal to or greater than 7 cm (1).

Figure 4. Character transformations used in a phylogenetic analysis of the paradoxidid trilobites. Character states correspond to adult morphology.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	ELRATHIA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	CENTROPLEURA	2	1	0	1	1	2	0	2	1	0	1	1	2	1	0	2	2	1	1	1	0	0	0	1
3	XYSTRIDURA	1	0	1	0	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0
4	PARADOXIDES	2	1	2	0	0	1	1	3	0	1	1	0	1	0	1	1	0	1	0	0	0	0	0	1
5	BERGERONIELLUS	0	0	0	0	0	1	1	1	?	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0
6	LERMONTOVIA	0	0	1	0	0	1	1	3	?	?	0	0	1	0	0	0	0	0	0	0	1	1	0	0
7	ANOPOLENUS	1	1	0	1	1	2	0	1	?	?	1	0	3	0	0	2	2	1	?	1	0	0	0	1
8	CLARELLA	2	1	0	1	1	2	0	1	?	?	1	1	3	1	0	2	2	1	?	1	0	0	0	1
9	GALAHETES	2	0	1	0	0	0	0	0	1	?	1	0	1	1	0	0	1	0	0	0	0	0	1	0

Figure 5. Data matrix of character states used in a phylogenetic analysis of selected paradoxidid trilobites. Elrathia is the outgroup.

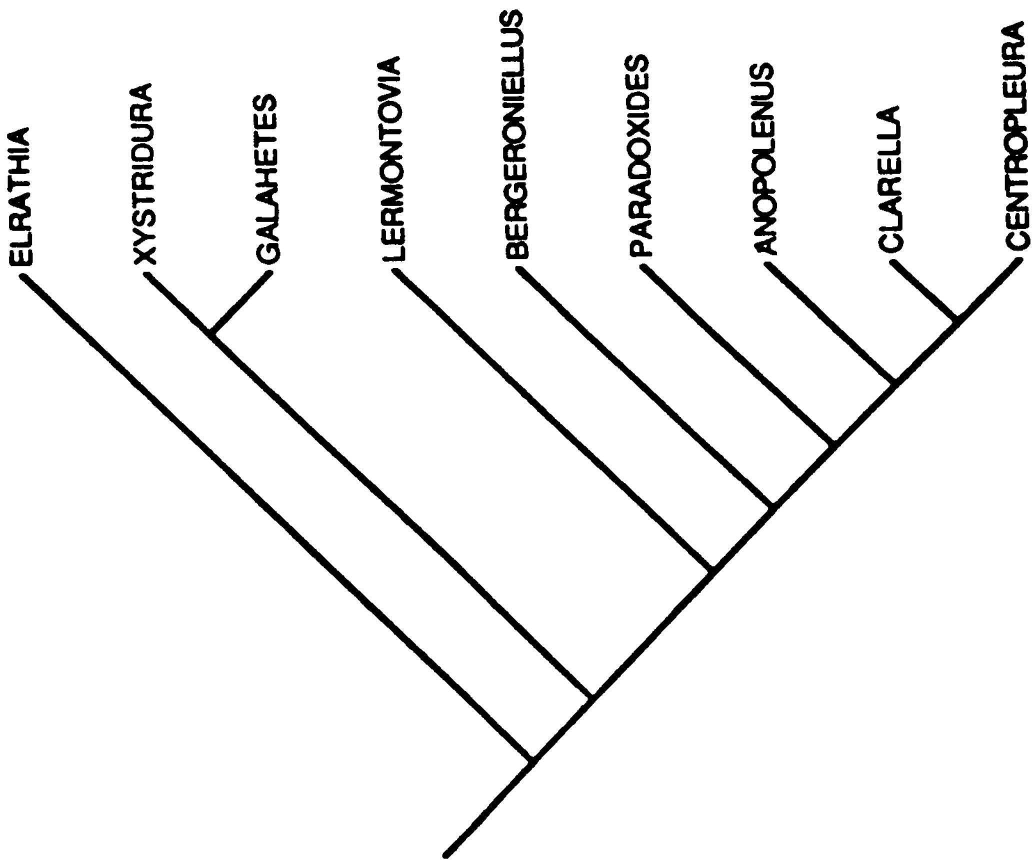


Figure 6. Single phylogenetic tree recovered for selected paradoxidid trilobites.

1) Glabellar morphology: short, anteriorly tapering (0), long, anteriorly tapering (1), long, parallel-sided to tapering (2), or figure eight-like shape (3).
2) Relative size of palpebral lobes: small (0) or large (1).
3) Preoccipital lobes: absent (0) or present (1).
4) Number of segments in thorax: 12-13 (0) or 9 (1).
5) Degree of taper of pygidial axis: moderate (0) or rapid (1).
6) Number of lateral glabellar furrows: 4 (0), 3 (1), 2 (2), 1 (3), or 0 (4).
7) Number of axial rings in pygidium: less than 10 (0), 10 to 12 (1), 12 to 13 (2), 11 to 14 (3), equal to or greater than 13 (4).
8) Relative width of axis: narrow (0) or moderately wide (1).
9) Length of genal spines: long (0) or reduced (1).
10) Eye ridges: present (0) or absent (1).
11) Interpleural furrows in pygidium: present (0) or absent (1).

Figure 7. Character transformations used in a phylogenetic analysis of selected Late Paleozoic trilobites of North America. Character states correspond to adult morphology.

		1	2	3	4	5	6	7	8	9	10	11	12
1	A.LODIENSIS	0	0	1	1	1	3	0	2	1	0	1	1
2	P.EURYBATHREA	0	?	1	?	0	0	1	2	1	?	1	1
3	B.SAMPSONI	2	1	1	1	0	0	1	1	1	1	1	1
4	P.CHESTERENSIS	1	1	1	1	0	1	0	4	1	0	1	1
5	A.MISSOURIENSIS	3	1	1	1	0	3	2	4	1	0	1	1
6	D.DECURTATA	1	1	1	1	0	2	0	1	1	0	1	1
7	D.SCITULA	1	1	1	1	0	2	0	3	1	0	1	1
8	K.CHESTERENSIS	1	1	1	1	0	3	0	1	1	0	1	1
9	G.BUFO	1	1	1	1	0	2	1	1	1	0	1	1
10	D.ROWI	2	1	1	1	1	0	0	1	1	0	1	1
11	E.KINGII	0	0	0	0	0	0	0	0	0	0	0	0

Figure 8. Data matrix of character states used in a phylogenetic analysis of selected Late Paleozoic trilobites of North America. Taxa analyzed are *Australosutura lodiensis*, *Piltonia eurybathrea*, *Breviphillipsia sampsoni*, *Paladin chesterensis*, *Ameura missouriensis*, *Ditomopyge decurtata*, *Ditomopyge scitula*, *Kaskia chesterensis*, *Griffithides bufo*, and *Dechenella rowi*. *Elrathia kingii* is the outgroup.

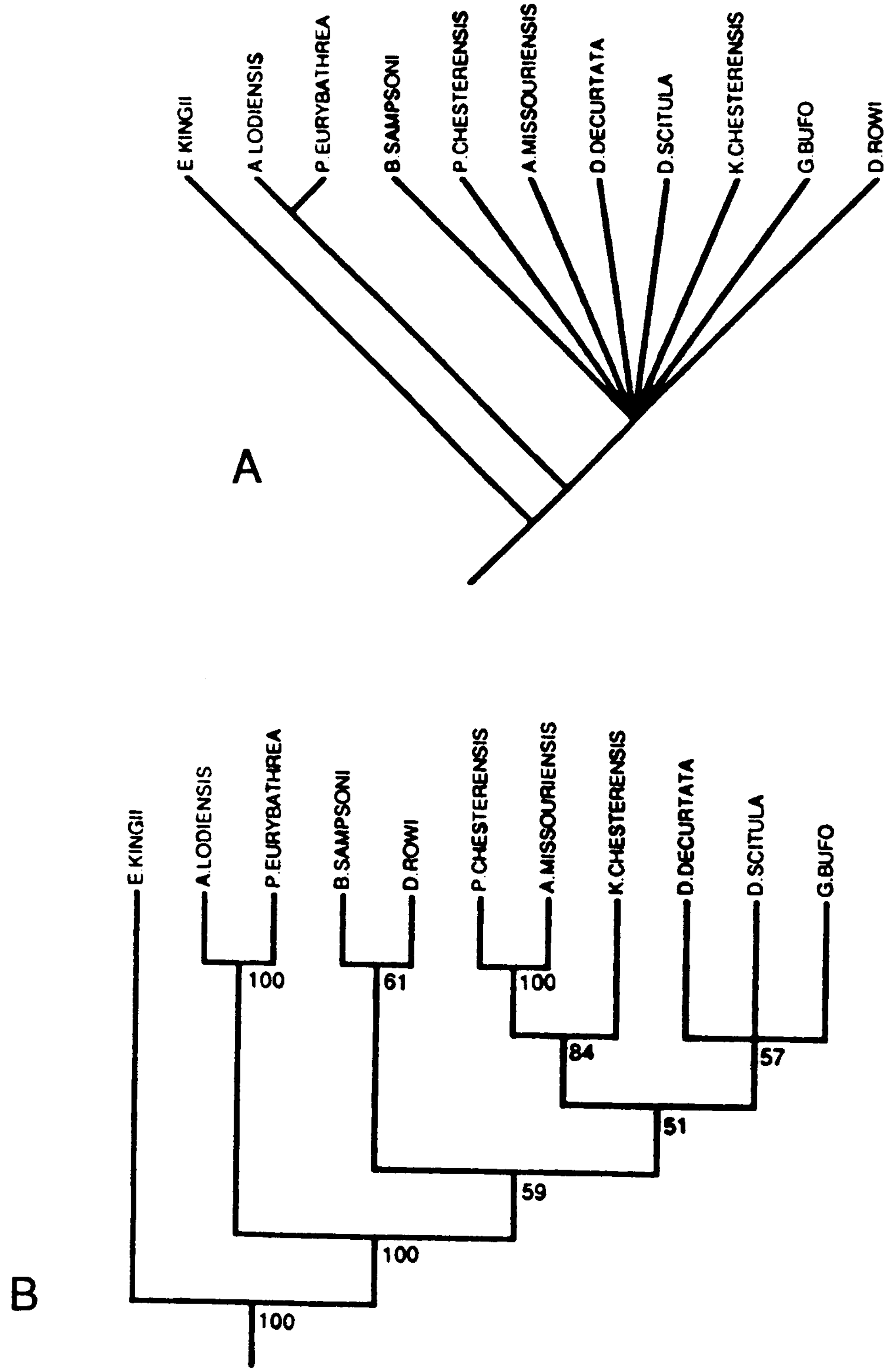


Figure 9. Strict consensus tree (A) and 50% majority rule tree (B) recovered in a phylogenetic analysis of selected Late Paleozoic trilobites of North America.

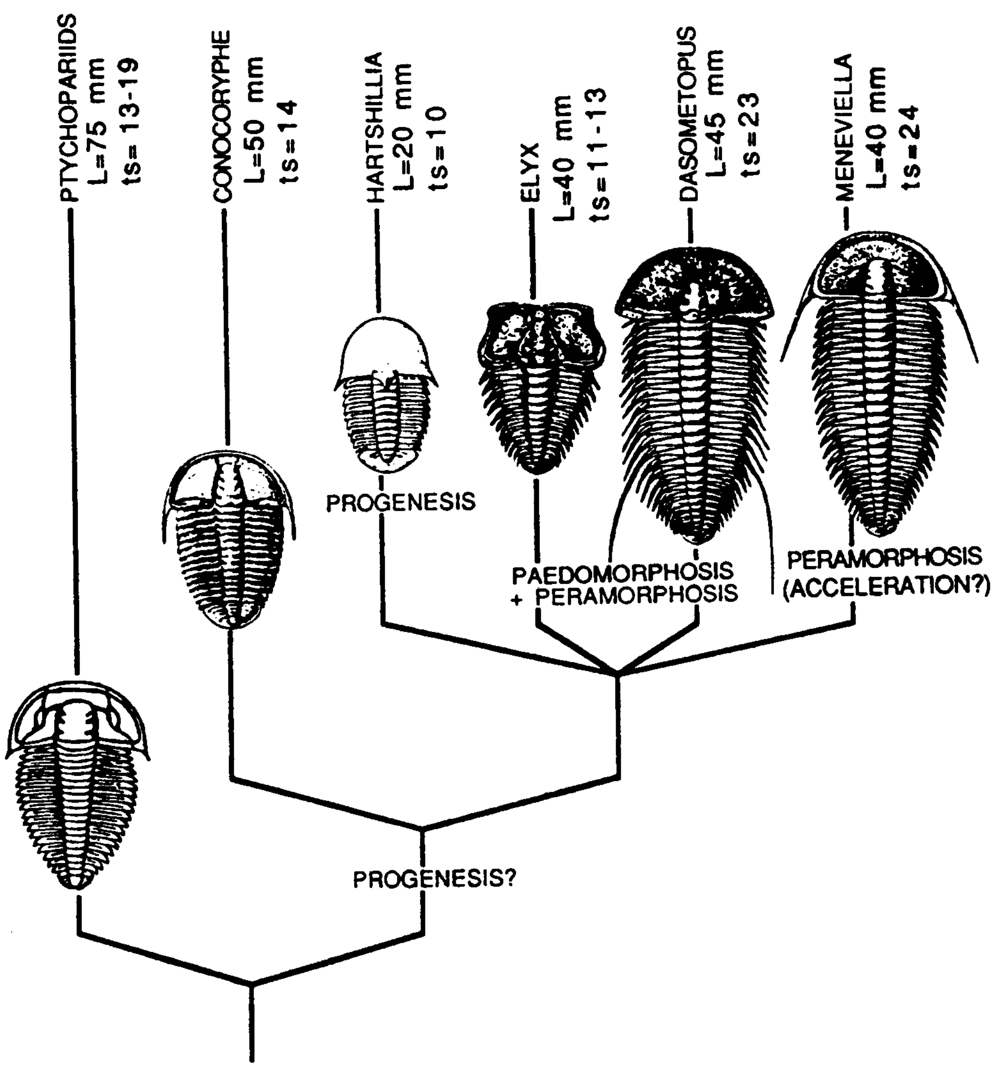
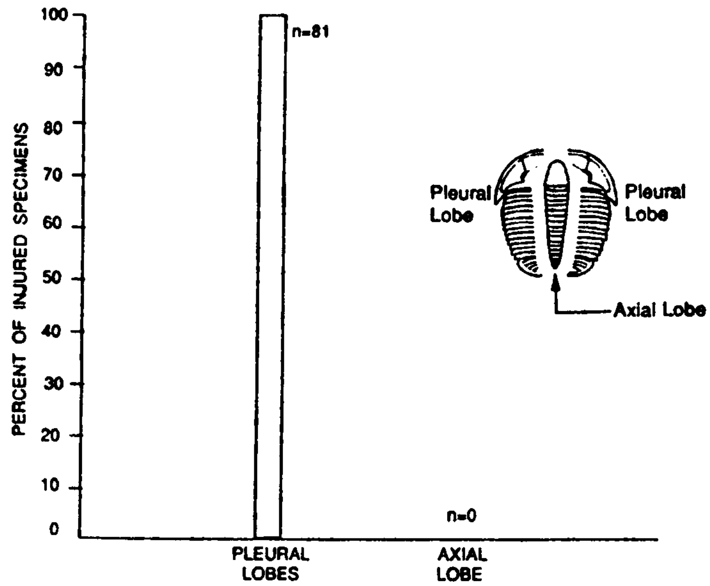


Figure 10. Suggested heterochronic processes involved in the evolution of selected conocoryphid genera, superimposed on an inferred phylogenetic tree. Symbols: L, maximum adult length; ts, number of thoracic segments.

A



B

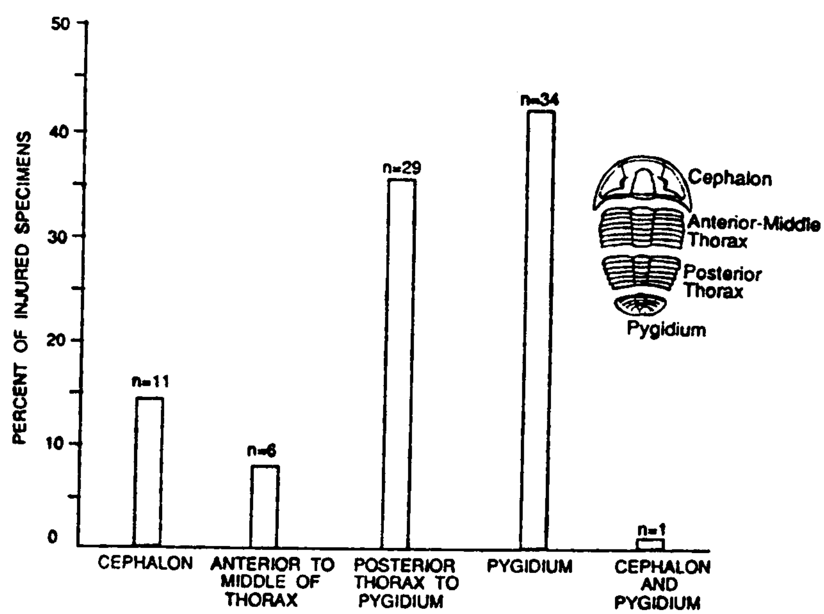
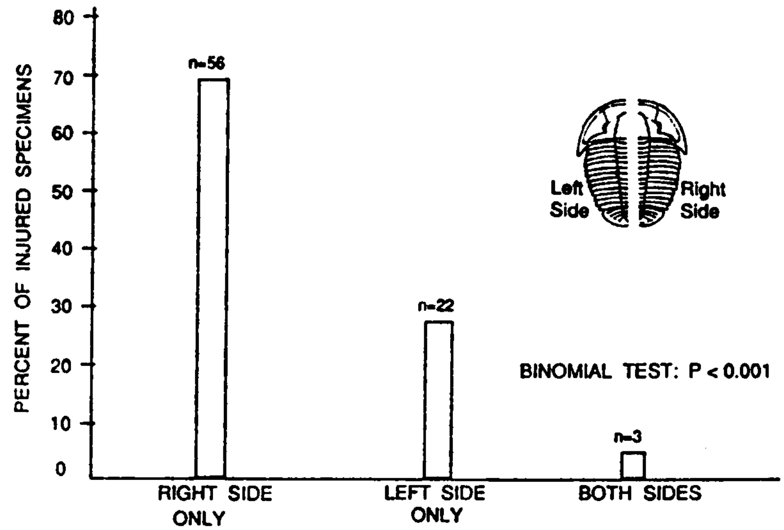


Figure 11. Locations of predation scars on trilobites, plus results of binomial tests. A, comparison of injuries to pleural lobes and axial lobes. B, Comparison of injuries to cephalon, thorax, and pygidium.

A



B

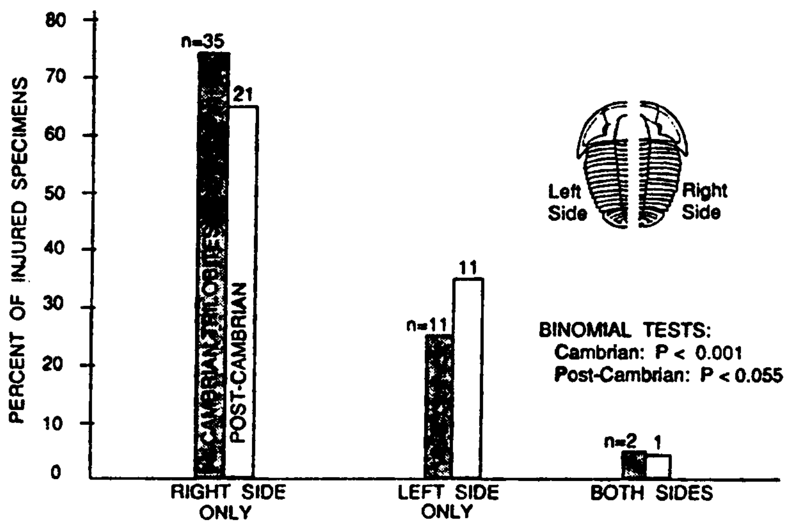


Figure 12. Locations of predation scars on trilobites, plus results of binomial tests. A, comparison of injuries to right, left, and both sides of all trilobites studied. B, comparison of injuries to right, left, and both sides of Cambrian and post-Cambrian trilobites.

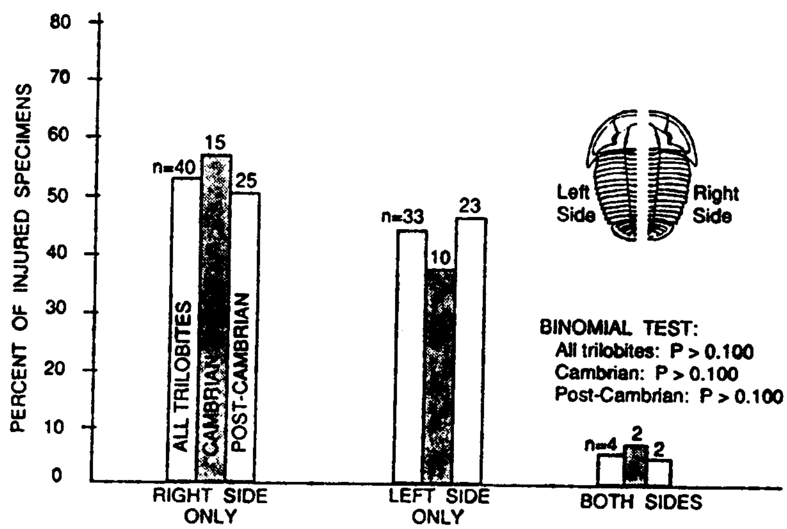


Figure 13. Locations of injuries of uncertain origin on right, left, and both sides of trilobites (all trilobites, Cambrian trilobites, and post-Cambrian trilobites), plus results of binomial tests.

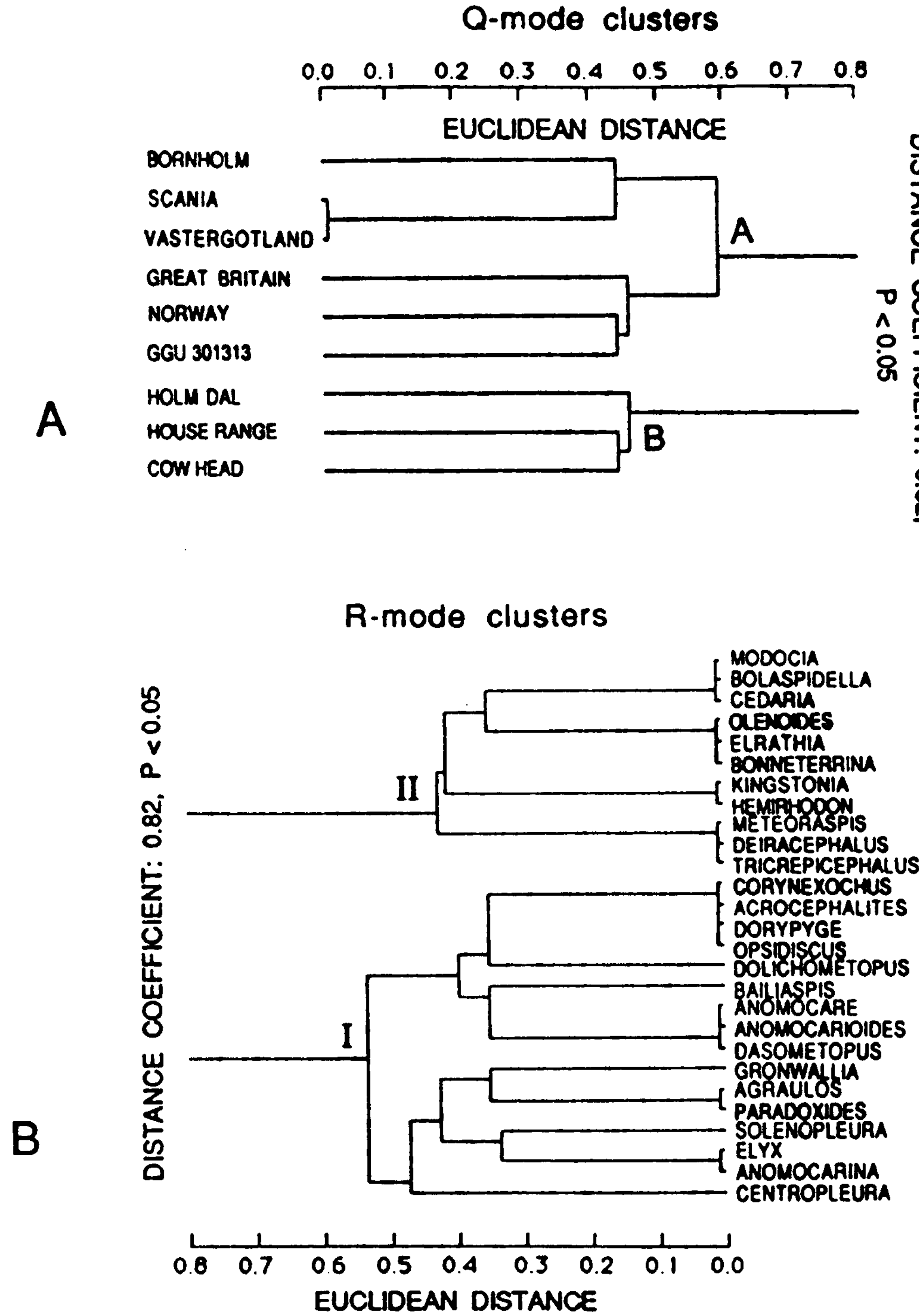


Figure 14. Results of Q-mode (A) and R-mode (B) cluster analyses performed on polymeroid trilobite collections from the <u>Lejopyge laevigata</u> Zone (Middle Cambrian) of North Greenland, North America, Scandinavia, and Great Britain. Meaningful clusters are labelled with capital letters or Roman numerals. Probability values are based on comparison to empirically derived distributions (data on probability distributions provided by C. G. Maples).

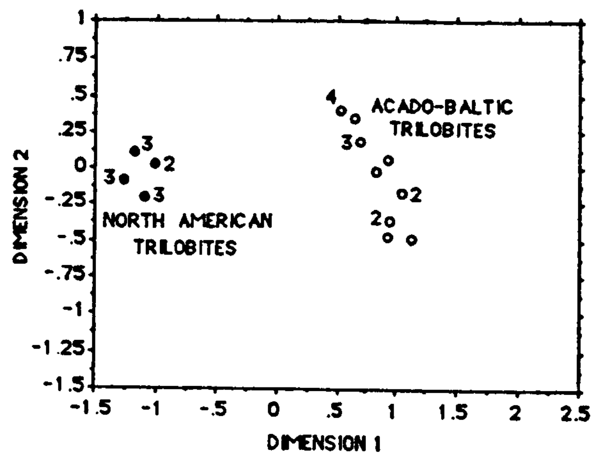
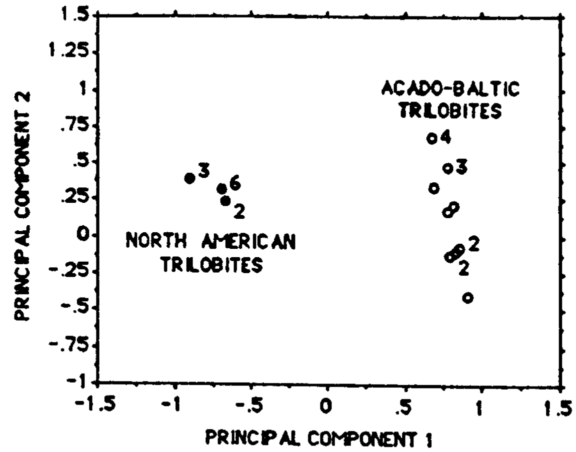


Figure 15. Results of multidimensional scaling of first two dimensions of data used to produce clusters in Figure 14A. Trilobites of North American aspect are indicated by solid circles and trilobites of Acado-Baltic aspect are indicated by open circles. The first axis is fitted primarily to a contrast between faunal associations and the second axis is fitted primarily to a contrast between more widespread and less widespread taxa.

A



B

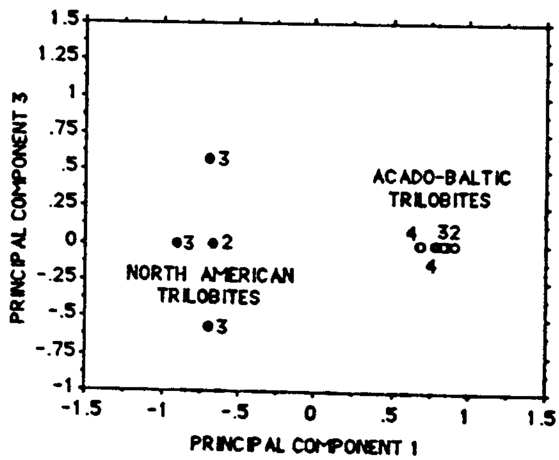


Figure 16. Results of principal components analysis of data used to produce clusters in Figure 14B. Trilobites of North American aspect are indicated by solid circles and trilobites of Acado-Baltic aspect are indicated by open circles. A, principal components 1 and 2. B, principal components 1 and 3. The first axis is fitted primarily to a contrast between faunal associations, the second axis is fitted primarily to a contrast between more widespread and less widespread taxa, and the third axis is fitted primarily to a contrast among some trilobites of North American aspect.

	CLUSTER A			CLUSTER B		
	F	C	N	F	C	N
Modocia	-	-	-	10	10	3
Bolaspidella	-	-	-	10	10	3
Cedaria	-	-	-	10	10	3
Olenoides	-	-	-	10	7	2
Elrathia	-	-	-	10	7	2
Bonneterrina	-	-	-	10	7	2
Kingstonia	-	-	-	10	7	2
Hemirhodon	-	-	-	10	7	2
Meteoraspis	-	-	-	10	7	2
Deiracephalus	-	-	-	10	7	2
Tricrepicephalus	-	-	-	10	7	2
Corynexochus	10	3	2	-	-	-
Acrocephalites	10	3	2	-	-	-
Dorypyge	10	3	2	-	-	-
Opsidiscus	10	3	2	-	-	-
Dolichometopus	10	5	3	-	-	-
Bailiaspis	10	7	4	-	-	-
Anomocare	10	5	3	-	-	-
Anomocarioides	10	5	3	-	-	-
Dasometopus	10	5	3	-	-	-
Gronwallia	10	7	4	-	-	-
Agraulos	10	8	5	-	-	-
Paradoxides	10	8	5	-	-	-
Solenopleura	10	10	6	-	-	-
Elyx	10	8	5	-	-	-
Anomocarina	10	8	5	-	-	-
Centropleura	10	8	5	-	-	-

Figure 17. Fidelity (F) and constancy indices (C) for polymeroids of the Lejopyge laevigata Zone in Q-mode clusters of Figure 14A. The number of collections containing a genus is listed under N. A hyphen (-) indicates the absence of a genus from a cluster.

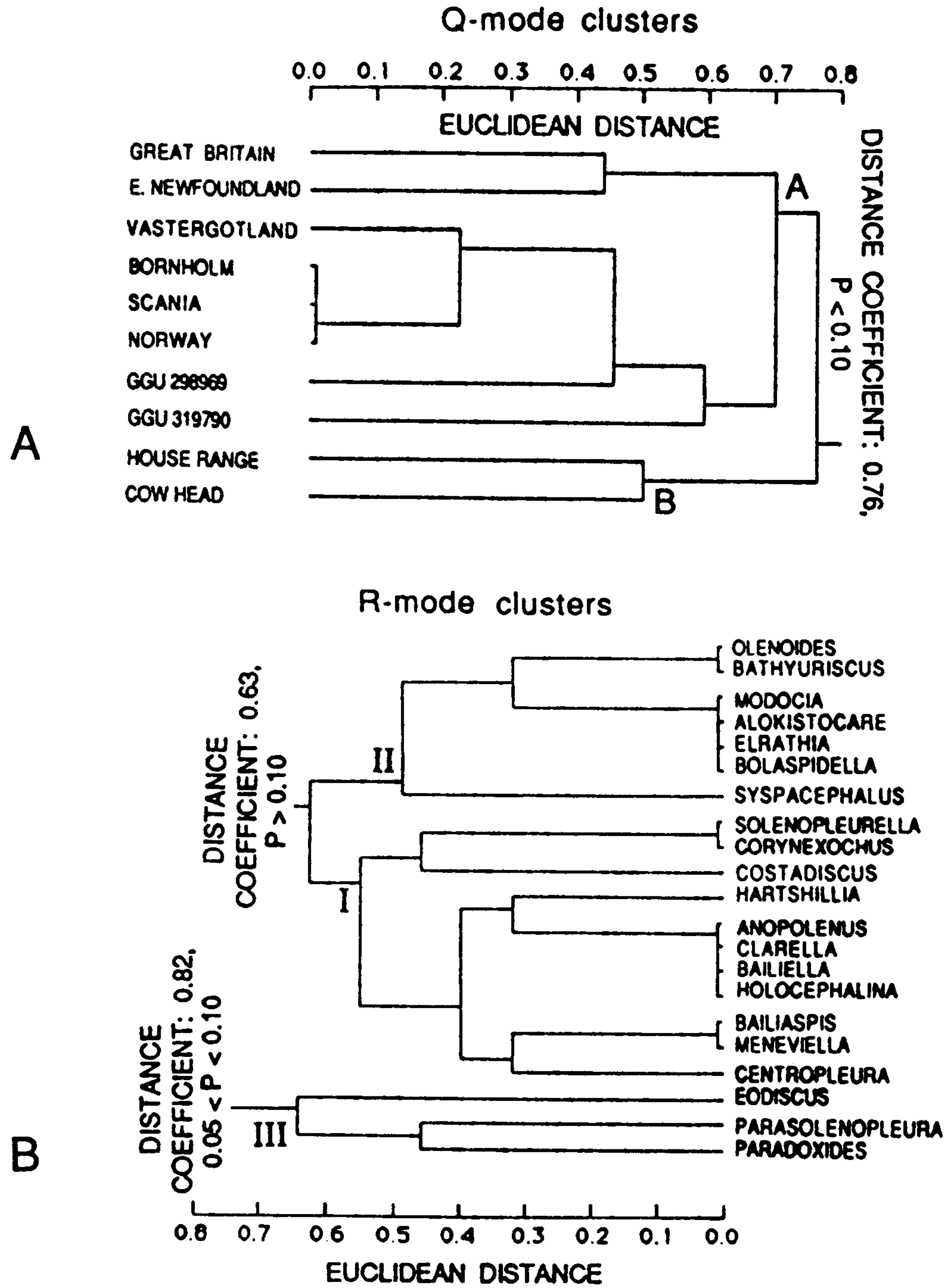


Figure 18. Results of Q-mode (A) and R-mode (B) cluster analyses performed on polymeroid trilobite collections from the Ptychagnostus atavus Zone (Middle Cambrian) of North Greenland, North America, Scandinavia, and Great Britain. Meaningful clusters are labelled with capital letters or Roman numerals. Probability values are based on comparison to empirically derived distributions (data on probability distributions provided by C. G. Maples).

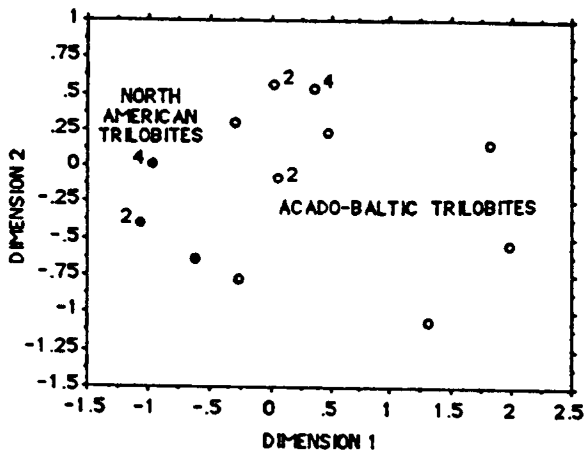


Figure 19. Results of multidimensional scaling of first two dimensions of data used to produce clusters in Figure 18A. Trilobites of North American aspect are indicated by solid circles and trilobites of Acado-Baltic aspect are indicated by open circles. The first axis is fitted primarily to a contrast between faunal associations and the second axis is fitted primarily to a contrast between more widespread and less widespread taxa.

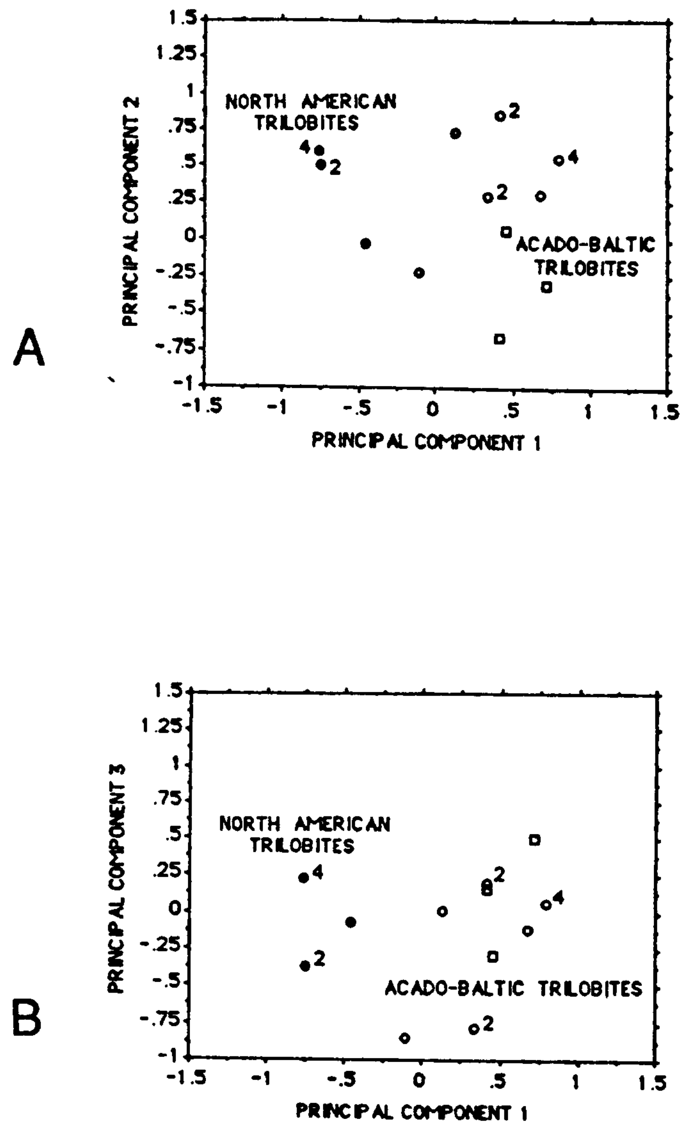


Figure 20. Results of principal components analysis of data used to produce clusters in Figure 18B. Trilobites of North American aspect are indicated by solid circles and trilobites of Acado-Baltic aspect are indicated by open circles and squares. A, principal components 1 and 2. B, principal components 1 and 3. The first axis is fitted primarily to a contrast between faunal associations, the second axis is fitted primarily to a contrast between more widespread and less widespread taxa, and the third axis is fitted primarily to a contrast between trilobites in mixed collections from putative continental slope deposits and unmixed collections.

	CLUSTER A			CLUSTER B		
	F	C	N	F	C	N
Olenoides	-	-	-	7	10	3
Bathyuriscus	-	-	-	7	10	3
Modocia	-	-	-	10	10	2
Alokistocare	-	-	-	10	10	2
Elrathia	-	-	-	10	10	2
Bolaspidella	-	-	-	10	10	2
Syspacephalus	-	-	-	5	5	2
Solenopleurella	10	3	2	-	-	-
Corynexochus	10	3	2	-	-	-
Costadiscus	10	3	2	-	-	-
Hartshillia	10	4	3	-	-	-
Anopolenus	10	3	2	-	-	-
Clarella	10	3	2	-	-	-
Bailiella	10	3	2	-	-	-
Holocephalina	10	3	2	-	-	-
Bailiaspis	7	3	3	-	-	-
Meneviella	7	3	3	-	-	-
Centropleura	5	1	2	-	-	-
Eodiscus	9	9	8	-	-	-
Parasolenopleura	10	8	6	-	-	-
Paradoxides	10	8	6	-	-	-

Figure 21. Fidelity (F) and constancy indices (C) for polymeroids of the Ptychagnostus atavus Zone in Q-mode clusters of Figure 18A. The number of collections containing a genus is listed under N. A hyphen (-) indicates the absence of a genus from a cluster.

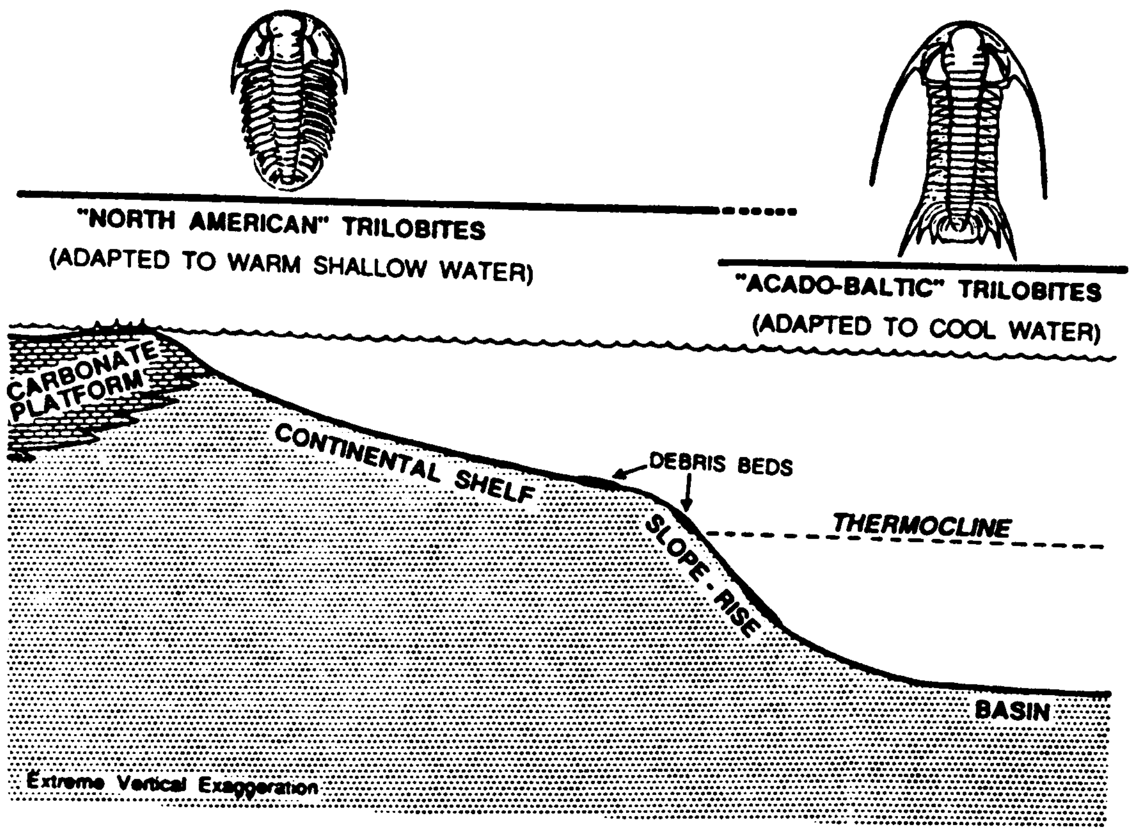


Figure 22. Model of the Innuitian margin of Laurentia during the Middle Cambrian illustrating the relationships of physiography, sedimentation patterns, and trilobite biofacies. Polymeroid trilobites of Acado-Baltic aspect are inferred to have lived below the permanent thermocline. Polymeroids of North American aspect are inferred to have lived in warm shallower water above the thermocline but their remains were probably washed downslope by gravity displacement of sediment (indicated by dotted lines and debris beds). Model based on stratigraphic, sedimentologic, and paleontologic evidence from North Greenland.