

2nd International Trilobite Conference (Brock University, St. Catharines, Ontario, August 22-24, 1997)

ABSTRACTS.

Characters and Parsimony.

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Character analysis is the single most important element of any phylogenetic study. Characters are simply criteria for comparing homologous organismic parts between taxa. Homology of organismic parts in any phylogenetic study is an a priori assumption, founded upon topological similarity through some or all stages of ontogeny. Once homologies have been suggested, characters are invented by specifying bases of comparison of organismic parts from taxon to taxon within the study group. Ideally, all variation in a single homology occurring within the study group should be accounted for. Comparisons are between attributes of homologous parts, (e.g., simple presence, size of something, number of something), and these attributes are referred to as character states. Study taxa are assigned membership in one (or more, in the case of polymorphisms) character-state for each character in the analysis. A single character now implies discrete groupings of taxa, but this in itself does not constitute a phylogeny. In order to suggest or convey phylogenetic information, the historical status of each character-state, and of the the group of taxa it suggests, must be evaluated. That is, in the case of any two states belonging to the same character, we need to discover whether one state is primitive (broadly speaking, ancestral) or derived (representative of an evolutionary innovation) relative to the other. This distinction - between special (apomorphic) versus general (plesiomorphic) similarity - is the fundamental property of cladistics. Because character states occur in a historical continuum, their status as apomorphies or plesiomorphies is relative. Once the relative historical status of character states has been determined, taxa with membership in these states assume hierarchical relationships, and an explicit phylogeny is thus inferred. Problems arise when different characters suggest different, contradictory, phylogenies. This inevitably occurs due to mistakes in assessing homology due to convergent evolution. It then becomes necessary to adopt an explicit criterion for selecting the best supported phylogeny from among the competing possibilities. Several candidates have been put forward, including some methods based on maximizing character compatibility (clique methods) and others based on the use of stratigraphic data. By far the most widely adopted, however, is a criterion of methodological parsimony. Parsimony is a principle of simplicity: all things being equal, the simplest explanation that is necessary and sufficient to fit a set of observations should be adopted. In science, this usually amounts to minimizing ad hoc hypotheses. In phylogenetic systematics, because we originally postulated all character states as putative homologies, when we choose among competing phylogenies we are necessarily introducing ad hoc assumptions that certain of the putative homologies (those not fitting the chosen phylogeny) should be reinterpreted as homoplasies. Methodological parsimony involves selecting that phylogeny which invokes the fewest number of ad hoc hypotheses of homoplasy. Because methodological parsimony involves minimizing something, there is a common misconception that the cladistic use of parsimony involves the assumption that evolution itself was always minimal, or parsimonious. This is not true. Only in specific, restrictive cases (for example, when cladograms are interpreted, usually to dubious ends, as complete, ancestral-descendant evolutionary trees) do methodological and evolutionary parsimony converge.

Early to Middle Ordovician trilobite-based biostratigraphic zonation of the Autochthon and Parautochthon, western Newfoundland, Canada.

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More than 100 species of Ordovician trilobites are known from the autochthonous / parautochthonous carbonate sequence of western Newfoundland. Altogether, fifteen trilobite zones are defined in the (uppermost) Port au Port, St. George and Table Head groups. These zones are based on more than 563 collections, which represent at least 487 horizons. Stratigraphic thicknesses of these zones range from a low of 4 metres in the St. George Group to a high of 215 metres in the Table Head Group. Each biozone (assemblage, interval, or lineage zone) is named for its most common or distinctive species. The base of each zone is defined by the first appearance datum (FAD) of this species; the top is defined by the base of the succeeding zone. Between 1976 and 1996, biostratigraphic data was obtained from the following areas: Port au Port Peninsula, Table Mountain, Goose Arm, Table Point, Hawkes Bay, Ingonchoix Bay, St. John Bay, Brig Bay, Boat Harbour, Cape Norman, Pistolet Bay and Hare Bay. The trilobite zones, in descending order, are:

Middle Ordovician Whiterockian Series No stages defined
Cybelurus mirus Interval Zone Pseudomera barrandei Interval Zone Uromystrum validum Interval Zone Bathyrurus perplexus Interval Zone Early Ordovician Canadian Series
Cassinian Stage Gignopeltis rarus Interval Zone Benthamaspis gibberula Interval Zone Strigigenalis caudata Lineage Zone Jeffersonian Stage Strigigenalis brevicaudata Lineage Zone Peltabellia knighti Assemblage Zone Demingian Stage Randaynia saundersi Interval Zone Hystricurus oculilunatus Interval Zone Gasconadian Stage Parahystricurus sp. I Assemblage Zone Hystricurus ellipticus Assemblage Zone Hystricurus millardensis Assemblage Zone Late Cambrian/Early Ordovician Gasconadian Stage Mississquoia typicalis Interval Zone

Nowhere in western Newfoundland is there continuous exposure of the biostratigraphic zonation, at least at surface. Furthermore, there are distinct faunal gaps at three levels: 1) between the Parahystricurus sp. I and Hystricurus oculilunatus zones; 2) between the Randaynia saundersi Zone and the Peltabellia knighti or Strigigenalis brevicaudata zones; and 3) between the Gignopeltis rarus and Bathyrurus perplexus zones. These faunal gaps are interpreted to represent significant regressive events.

The utility of the Canadian Series and a proposed trilobite-defined base for the Cassinian Stage.

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The suggestion that the 'Canadian Series' be suppressed in favor of the 'Ibexian Series' is regarded as premature. Trilobite faunas of the component stages of the Canadian Series are readily identified and correlated along the Caledonide-Appalachian-Ouachita orogenic belt, from northwest Scotland to Oklahoma. These trilobite faunas, however, are less easily correlated with those of the Ibexian Series type area, as others have pointed out. Consequently, separate Series designations may be required for eastern and western North America. The first appearance datum (FAD) of *Strigigenalis caudata* (Billings, 1865) in western Newfoundland, (i.e., the base of the *Strigigenalis caudata* Lineage Zone) is proposed as a candidate for the base of the Cassinian Stage of the Canadian Series. *Strigigenalis caudata* (Billings, 1865) is an extremely widespread species, occurring in western Newfoundland, Qu'bec, Pennsylvania, Missouri-Arkansas and Oklahoma.

Late Canadian (Latest Jeffersonian to Cassinian) trilobite biofacies of the St. George Group, western Newfoundland, Canada.

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The Barbace Cove Member of the Boat Harbour Formation is a Late Canadian (latest Jeffersonian to Cassinian) sequence of cyclic shallowing upward peritidal carbonates. The overlying Catoche Formation consists largely of subtidal limestones. Biofacies analysis of the contained trilobites indicates that, altogether, five distinct biofacies may be recognized in these carbonate units. The *Peltabellia* Biofacies and the *Isoteloides-Strigigenalis* Biofacies are relatively low diversity biofacies that are developed in (commonly) rippled intertidal grainstone and packstone beds and lenses. The *Peltabellia* biofacies is dominated by species of *Peltabellia*; high spired gastropods are also abundant. This biofacies may be recognized at Boat Harbour, Eddies Cove West and Barbace Point (Port au Choix Peninsula). It is also developed in the Poulsen Cliff Formation, north Greenland. The regionally widespread *Isoteloides-Strigigenalis* biofacies is dominated by the nominate genera. *Bolbocephalus* also forms an important component, and articulate brachiopods are often abundant. This biofacies is recognizable on the Brent Islands (Hare Bay), Schooner Island (Pistolet Bay), at Boat Harbour, Eddies Cove West, Barbace Point and Catoche Point (Port au Choix Peninsula) and The Gravels (Port au Port Peninsula). This biofacies also appears to predominate in the Fort Cassin Formation of the Champlain Valley and the Axemann Limestone of Pennsylvania. The *Randaynia* biofacies of the Barbace Cove Member of the Boat Harbour Formation and the *Illaenus-Bolbocephalus* biofacies of the Catoche Formation are restricted to lime boundstone with lime packstone and grainstone interfill. The lime packstone and grainstone interfill, the generally large, dominantly thrombolitic microbial mounds, and high faunal diversity indicate a moderate-energy subtidal environment. The older *Randaynia* Biofacies is characterized by an abundance of *Randaynia langdoni* Boyce, 1989. This biofacies is only recognized at Boat Harbour. The younger *Illaenus-Bolbocephalus* Biofacies is characterized by abundant *Illaenus* sp. nov. and *Bolbocephalus kindlei* Boyce, 1989. The presence of *Kawina* in this biofacies strongly suggests open ocean conditions. This biofacies is best developed on Burnt Island and Schooner Island (Pistolet Bay), but is locally recognizable in the Canada Bay area, at Catoche Point (Port au Choix Peninsula) and Eddies Cove West. The *Jeffersonia* Biofacies is developed in bioturbated lime mudstone and wackestone, and is characterized by abundant *Jeffersonia* species and less common *Ischyrotoma*. In the Barbace Cove Member of the Boat Harbour Formation *Grinnellaspis* approaches *Jeffersonia* in abundance. This biofacies is regionally widespread and is typical of the Catoche Formation; older examples of the *Jeffersonia* Biofacies feature equally abundant *Uromystrum*, whilst younger examples feature *Bathyuirellus* instead. The bioturbation and high faunal diversity indicate a quiet, subtidal shelf environment.

Exuviation and extinction.

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Trilobite extinction is enigmatic. The usual litany of environmental agents of extinction: climate change, meteorite impact, and sea-level fluctuation/habitat destruction do not provide an overarching hypothesis for the decline and ultimate demise of the trilobites, because (1) there is not a clear correlation of an environmental agent with every trilobite extinction, (2) there are episodes of environmental change for which there are no trilobite extinctions, (3) other macro-benthic marine arthropods (crabs, shrimp, lobsters, horseshoe crabs) living in similar habitats and occupying similar (although temporally disparate) niches have not suffered the same fate. Biological factors, especially the evolution and expansion of potential predator groups, probably contributed to the inability of trilobites to recover from the successive extinctions that decimated trilobite taxa after the Middle Cambrian. Diversity diagrams show the initial mid-Cambrian decline of trilobites coincident with the initial diversification of cephalopods, which have long been regarded as potential trilobite predators. Other arthropods (e.g., *Anomalocaris* in the Middle Cambrian) and fish were also likely predators on trilobites. Cephalopods and fish diversified as trilobites declined during the Devonian and later Paleozoic. Predation by itself might not be sufficient cause to precipitate the extinction of an entire class of arthropods. Modern groups (crabs, shrimp, lobsters) thrive even in the face of flourishing predator groups. Malacostracans enjoy an adaptive radiation that started in the Mesozoic and continues today, and is reflected in great morphological and ecological diversity. Also successful, as measured by geological persistence, if not by morphologic and taxonomic diversity, are the xiphosurans (*Limulus*). This chelicerate persists in comparative taxonomic, ecologic, and morphologic monotony from the Paleozoic to the present. The differential evolutionary success of these three arthropod groups suggests a line of investigation that may illuminate the question of the ultimate demise of the extinct group: Is there an attribute shared by the conservative xiphosuran and the diverse malacostracans, but absent in the trilobites, that might contribute to the success of the former two groups and the extinction of the latter? Modern marine arthropods are characterized by consistent molt patterns; crabs, shrimp, lobsters, and horseshoe crabs each have a "set" or signature ecdysial style. Conversely, there is not "trilobite style" of molting; rather, trilobites are characterized by a range of molt configurations, and this variation exists within individual species. Eighty-to-90 percent of modern arthropod mortality occurs during molting, from increased vulnerability to predators during the soft-bodied phase or from accidents in shedding the old exoskeleton. A set ecdysial habit may be more efficient (e.g., provide for faster egress from the old exoskeleton) and less prone to accidents of not cleanly discarding molt elements, and thus prove to be an advantage over a less-organized ecdysial habit. Thus, the cumulative effect of a less-than-optimal ecdysial habit, accompanied by the diversification of potential trilobite predators during the Paleozoic, are compelling biotic factors to consider in explaining the ultimate demise of the Trilobita.

The Walcott-Rust Quarry: A Middle Ordovician trilobite Konservat-Lagerstätte.

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In 1873 an aspiring paleontologist, C. D. Walcott, discovered a unique trilobite bed in the Middle Ordovician Trenton Group limestones. Stimulated by Louis Agassiz, Walcott began a series of investigations which set his career on path. Re-excavation of the Walcott-Rust quarry by T. Whiteley has yielded abundant new material and revealed details of taphonomy and paleontology of the site. The quarry is in the lower third of the Rust Limestone Member of the Denley Formation. This part of the Trenton Group is of late Shermanian (middle Caradocian) age near the *Corynoides americanus* to lowest *Orthograptus ruedemanni* graptolite zone boundary. Most of the Rust is composed of a monotonous series of fossil rich but heavily bioturbated limestones (skeletal wacke- to packstones). Correlation of the quarried section with outcrops in the gorge of West Canada Creek indicates that these form one part of a distinctive fine grained interval, the Prospect Beds, about 12 meters above the base of the Rust Member, which sharply overly a coarse packstone interval at an apparent marine flooding surface (minor transgression). The limestones of the quarry are, for the most part, lightly burrowed but not bioturbated micrites suggesting a series of rapid burial events with relatively little time interval in between. They display sharp bases, with some evidence of scour, fining upwards into micrites. Tops are irregular, burrowed and may display thin skeletal hash beds. Limestone beds are separated by brownish gray, calcareous claystones (shales). With the exception of one layer, few of the well preserved trilobites are on bedding planes, rather they often occur within the beds perhaps indicating that they were transported locally by the limey mud flow composing the turbidity currents to yield fossil rich "obtrusion event beds". A one meter interval of micritic limestones at the Walcott-Rust quarry has yielded well preserved remains of over 73 species of fossils, including at least 15 species of trilobites (although 25 different trilobite species have been named from the site, some appear to be junior synonyms). One 1 to 5 cm thick bed, features partially enrolled trilobites in which appendages are preserved. Specimens from this bed were used by Walcott for the first definitive description of appendages on trilobites. Three species with appendages were found in this layer, *Ceraurus pleurexanthemus*, *Flexicalymene* cf. *F. senaria* and *Primaspis trentonensis*. The trilobite appendages have been uniquely preserved by infilling with calcite. The first phase of cement formed a series of discontinuous thin (10 μ m) patches of fibrous calcite. This was followed by an isopachous fringe lining the inside of the limbs and carapace. The subsequent cavity was infilled by spar calcite and aborescent growth of pyrite. The latter may be replacing microbial colonies.

Macroevolutionary patterns of Late Paleozoic trilobites of the United States.

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Based on species ranges, four stages of evolution can be recognized for Carboniferous and Permian trilobites of the United States. Stage 1 is present within Lower Carboniferous strata and is comprised of three separate faunas. The lowest fauna is dominated by *Breviphillipsia sampsoni* and is present in late Kinderhookian (Tournaisian) rocks. The middle fauna contains *Breviphillipsia semiteritis* and is present in early Osagean (late Tournaisian) strata. The upper fauna contains *Exochops portlocki* and is present in late Osagean to early Meramecian (early Viséan) strata. Stage 1 is characterized by strongly endemic, stenotopic species that were niche-specific and exhibited a well-developed generic onshelf to offshelf segregation. Stage 2 is present in Meramecian (late Viséan) through Chesterian (Namurian) rocks and is dominated by species of the pandemic genus *Paladin*. Within Stage 2 species tend to be long-ranging and eurytopic, occurring in a wide range of depositional environments. Stage 3 is present in Morrowan through early Permian strata and consists of three faunas. The lowest fauna is made up of the genus *Sevillia*, and is present in Morrowan (late Namurian) through Atokian (Westphalian) rocks. The middle fauna is comprised of *Ditomopyge scitula* and ranges from Desmoinesian (late Westphalian) through Missourian (Stephanian). The upper fauna is made up of *Ditomopyge decurtata* and extends from the lower Virgilian (Stephanian) to early Leonardian (late Sakmarian-early Artinskian). Species of Stage 3 are very long ranging and characteristically eurytopic. Stage 4 is present within late Leonardian through Guadalupian (Kazanian) rocks and is characterized by the short-ranging genera *Delaria* and *Anisopyge*. Stage 4 genera and species are strongly endemic and typically associated with shelf margin environments. These species were stenotopic, typically occurring within brachiopod and reefal biofacies. The four-stage evolutionary development of Late Carboniferous trilobites from the United States is interpreted to have been significantly controlled by second- and third-order sea level changes. Stage 1 is interpreted as an adaptive radiation during flooding of the Kaskaskia sequence (second-order sea level cycle) and itself represents a third-order cycle. Each individual fauna is controlled by the distribution of fourth-order sea level changes. The eurytopic species of Stage 2 appear to be well adapted to the changing environmental conditions that occurred during regression of the Kaskaskia sequence when minor (fourth- and fifth order) sea level changes characterized the sedimentary record. Similarly, Stage 3 species were eurytopic and existed in a wide range of environments during the rapidly changing environmental conditions of the Absaroka transgression (second-order) when third- fourth- and fifth-order sea level fluctuations were prominent. These hearty species were long-lived owing to their tolerance of rapidly changing environmental conditions and ability to inhabit a broad variety of environments. Regression of the Absaroka Sequence during the Permian created Stage 4. Most of the members of this stage are known only from the shelf-edge, reefal and basinal environments of West Texas. Destruction of the basinal environments during the Late Permian eliminated refuges from which previous adaptive radiations had originated and thereby led to the final extinction of trilobites.

Phylogenetics: A Primer of Phylogenetic Procedures.

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During the past decade it has become increasingly apparent that reference to an explicit hypothesis of phylogenetic relationships is a necessary starting point for any evolutionary study. The method of choice for producing phylogenetic hypotheses is phylogenetic systematics *sensu* Hennig. This approach comprises a 6-part process: (1) assemble information about as many features as possible for the members of a study group (the ingroup); (2) compare the various features of each member, assuming a priori that close similarity = homology; (3) determine which of the various presumptive homologous states for each set of features is plesiomorphic (ancestral for the ingroup) using outgroup comparisons; (4) make groups of members of the ingroup based on shared non-plesiomorphic traits (synapomorphies); (5) when there are conflicts in the groupings postulated by the putative synapomorphies, choose the groupings that are supported by the largest number of synapomorphies; (6) re-interpret, a posteriori, traits that are inconsistent with the best-supported hypothesis, as homoplasies. Phylogenetic systematics avoids the risk of circularity in constructing phylogenetic hypotheses, but in doing so gives up a strong (a priori) homology criterion for the relatively weak one of taxonomic congruence. Most practical problems with phylogenetic analyses occur when (1) not enough characters are used, (2) the ingroup is not monophyletic, (3) more than 1 apomorphic state occurs in the ingroup (multi-state characters), or (4) more than 1 feature occurs in the ingroup and the outgroups. The first 2 problems become apparent, and correct themselves, during the course of most studies. The third is solved by functional outgroup analysis (unordered states in computer assisted analyses). The fourth is solved by the use of multiple outgroups.

Functional morphology of Phacopinae and the mechanics of enrolment.

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Large collections of phacopids have been prepared mechanically and serially sectioned to understand enrolment strategies. It is concluded that enrolment was for protection and was provoked by any event leading to changes in water and sediment movement. Preparation of ventral surfaces of Geesops from the Lower Eifelian of Germany show the morphology of paired apodemes on each thoracic segment, two pairs on the cephalon and one pair on the pygidium. A model of muscle attachment for limbs and an enrolment mechanism is presented. During enrolment, gliding of pleurae takes place along cone surfaces which intersect a sphere. Surfaces on cone and sphere are modelled to explain this and surface configurations are confirmed by contouring using the method of Moire topography. Interpleural articulation combines movement between and anterior articulation groove and axial process and a posterior flange and socket with both structures lying along the same axis of rotation. Study of coaptative structures on other phacopids has allowed the recognition of four basic types of pleura termination. The tenon-like tip in Eophacops (Silurian) becomes modified in Paciphacops (Silurian-Devonian) with the formation of a vincular hook. Phacops s.l. has a vincular boss which in Reedops s.l. (Devonian) becomes reduced. The vincular notch is modified to fit these respective structures.

The Ontogeny and Phylogeny of Lichids.

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The silicified trilobite fauna of the Avalanche Lake area of the Mackenzie Mountains, Northwest Territories, Canada contains a diversity of lichid taxa, including the protaspides and meraspides of five genera from three subfamilies, the Lichinae, Homolichinae and Trochurinae. At the generic level, this more than doubles the number of known lichid ontogenies. Present knowledge of lichid systematics and phylogenetic relationships has been based entirely on holaspid morphology. Ontogenetic sequences and larval forms can provide important information regarding phylogenetic relationships, particularly in determining membership in higher taxa, since highly derived characters found in the adult may not yet be present in the early stages. A cladistic analysis, using PAUP 3.1, based on the last protaspid instar of all well-described lichid protaspides from this study and from the literature includes *Dicranopeltis*, *Platylichas*, *Amphilichas*, *Acanthopyge*, *Borealarges*, *Dicranogmus* (two species), *Hemiarges* (three species) and *Radiolichas*. The cladogram shows that the lichids are a monophyletic taxon, but divisions into subfamilies, as determined by holaspid morphology, are not supported. Most of the lichid taxa included in the analysis are members of the Subfamily Trochurinae which, in this analysis, is not a monophyletic group. *Dicranopeltis*, *Platylichas*, *Amphilichas*, *Dicranogmus* and *Radiolichas* form a terminal clade. This would seem to lend support to the idea that *Dicranogmus* and *Radiolichas* are improperly placed in the subfamily Trochurinae, but their position remains ambiguous. *Dicranogmus* and *Radiolichas* are separated from adjacent taxa by a number of synapomorphies. The outgroup taxa have an influence on the internal arrangement of this part of the cladogram, with *Acanthopyge* and *Borealarges*, undisputed trochurines, moving in and out of this terminal clade, depending on the outgroup taxa used. In the literature several candidates, including odontopleurids, illaenids, styginids and proetids, have been proposed as the sister group of the lichids, with the odontopleurids being the most favoured. In this analysis based on the last protaspid instar, up to seven outgroup taxa selected from the proposed sister groups, are used. The results show the odontopleurids are not the sister group. However determining what is the sister group is more difficult. One of the proetids, *Dimeropyge* occupies the sister group position on this cladogram, but there are problems. The proetids are not monophyletic according to this analysis, and the proetid protaspides are missing a number of characters and are added to the base of the tree according to "rooting implied by tree description". The resolution of difficulties in the present classification of lichids and in the identification of the sister group of lichids will require information from all ontogenetic stages.

Proetida, an orderly or disorderly order of trilobites: evidence from the larvae.

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When Richard Fortey and Bob Owens proposed a new Order Proetida at the last International Conference on Trilobites in Oslo, they used "morphological features and ontogeny". The small growth stages they used were primarily small meraspid cranidia. It is generally acknowledged that larval morphologies are useful in recognition and determination of higher taxa. Jan Bergström attacked the concept of an Order Proetida, pointing out that it included taxa showing more than one pattern of enrollment. Fortey and Owens responded that some trilobite species enroll in more than one manner, and so enrollment is not necessarily an important character at ordinal level. In the intervening decades, larval (protaspid) information has been gathered (in most cases published) for a number of taxa included in Proetida, including: Bathyrurus, Carolinites, Carrickia, Cyphaspid, Devonoproetus, Dimeropyge, Goniophrys, Hyperbolochilus, Hystricurus, Licnocephala, Oosites, Scharyia, Telephina, Parahystricurus, 'Paraplethopeltis', Paratoernquistia, Songkania, and Stenoblepharum. There is considerable morphological variation among protaspides assigned to the taxa listed above. Almost all proetide ontogenies start with a protaspid where the protopygidium can not be distinguished from the protocranidium (an 'anaprotaspis'). The morphologies of these anaprotaspides vary considerably. Some proetide ontogenies include a radical metamorphosis within the protaspid period, and others undergo much less radical changes. Where radical metamorphoses occur within the ontogeny, they are usually directly associated with a radical change in the life style of the individual (often from planktonic to benthic?). Some taxa have a distinct sculpture of enlarged tubercles in later protaspides (metaprotaspides) and early meraspides, and others show no evidence of such a sculpture. Despite the presence of at least two radically different types of 'anaprotaspides' in different groups of Proetida, some members of the Telephinidae appear to include both types within the same ontogeny, suggesting that this may not reflect distant ancestry of these two groups. There appears to be far less variation among larvae assigned to the Lichida or the Odontopleurida than among those assigned to the Proetida. If the Order Proetida is monophyletic, it should be possible to find synapomorphies that may be used to characterize the order, and are not shared by members of the Ptychopariida, that includes its probable ancestors. Features used to recognize proetide larvae are discussed, with particular attention paid to their relevance to answering the question as to whether or not the Proetida is monophyletic.

Stratigraphy and Trilobite faunas of the Mungog Formation (Lower Ordovician), Yeongweol, Korea.

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The Cambrian-Ordovician sedimentary rocks in southern Korea, which are called the Joseon Supergroup, have been conventionally differentiated into five types of sequences based on their unique lithologic successions and geographic distribution: namely, Duwibong, Yeongweol, Jeongseon, Pyeongchang, and Mungyeong sequences. The Mungog Formation occupies the Lower Ordovician portion of the Yeongweol sequence and has been known to yield relatively diverse invertebrate fossils. It consists mostly of carbonate with lesser amounts of shale, representing a supratidal to subtidal environment. The formation is subdivided into four members based on the association of dominant lithofacies such as ribbon rock, grainstone to packstone, flat-pebble conglomerate, and marlstone to shale facies: i.e., Garam, Baeiljae, Jeommal, and Dumog Member in ascending order. The basal Garam Member consists mainly of ribbon rock and grainstone to packstone facies with occasional intercalations of thin flat-pebble conglomerate beds. Trilobites and brachiopods occur at the lowermost several-m-thick interval of the member. The succeeding Baeiljae Member is recognized by the occurrence of a thick (30-35 m in thickness) sequence of massive dolostone and no fossils have been recovered from this member yet. The Jeommal Member is characterized by alternations of ribbon rock and flat-pebble conglomerate lithofacies with occurrence of grainstone to packstone beds in the uppermost part. *Kainella*, the only known trilobite of the member, is found from the lowest bed (ca. 30 cm thick) of the member. The Dumog Member comprises diverse lithofacies including marlstone to shale, flat-pebble conglomerate, grainstone to packstone and ribbon rock facies, and is distinguished from other members by frequent intercalations of greenish gray marlstone to shale beds. Trilobites are the dominant fossil group in this member, although brachiopods, ostracods, pelmatozoan stems, and fossils of uncertain zoological affinity are also frequently observed. Trilobite occurrences in the Mungog Formation are confined to the three stratigraphically separated intervals which are herein referred to the *Yosimuraspis vulgaris*, *Kainella euryrachis*, and *Shumardia pellizzarii* zones, respectively. The *Yosimuraspis vulgaris* Zone at the basal part of the Garam Member consists predominantly of *Yosimuraspis* and subordinately of *Jujuyaspis* and *Pseudokainella*, and indicates an early Tremadoc in age. Comparable faunas are well represented in North China. The *Kainella euryrachis* Zone represented solely by the nominal species can be correlated with the middle Tremadoc of North America and Argentina. The *Shumardia pellizzarii* Zone comprises a number of cosmopolitan trilobite taxa such as *Micragnostus*, *Asaphellus*, *Shumardia*, *Hystricurus*, *Apatokephalus*, and *Dikelokephalina* with endemic species such as *Koraipsis spinus* and *Hukasawaia cylindrica*. It is closely comparable to the Dumugol fauna of the Duwibong sequence in Korea and late Tremadoc faunas of North China and Australia.

Evolutionary dynamics of olenid trilobites in the upper Cambrian of southern Sweden.

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The upper Cambrian Alum Shales of Scandinavia are well developed (50m thick) in southern Sweden. Olenid, and some agnostid trilobites occur in immense numbers, and often at all growth stages. In the black shales they are flattened, but they are especially well preserved in three dimensions in concretions. The old quarries at Andrarum provide a fine natural laboratory for studying evolutionary patterns and processes within the single, well-defined family Olenidae. Rate of turnover is high in these condensed successions and 6 biozones, with 31 subzones have been defined. We have made detailed studies of the ontogeny of *Olenus* (mainly from isolated tagmata) and the descendant *Parabolina* (where the juveniles are often complete). Comparative ontogeny shows that most features of *Parabolina* are of paedomorphic origin; reduction of the preglabellar field, retention of the visual surface and conterminant hypostome, yoking of the librigenae, position of eyes, spinosity of thorax and pygidium, more numerous glabellar furrows and reduction in number of thoracic segments. The origin of *Parabolina* is best considered as a mosaic paedomorphocline. Complementary studies of evolution within *Olenus* from flattened specimens in shale confirm Kaufmann's (1933) demonstration of a gradualistic lengthening and narrowing trend in pygidial shape. If this is truly microevolutionary, then the data is consistent with Sheldon's view that persistent phyletic evolution is characteristic of narrowly fluctuating, slowly changing environments. Analysis of successive bedding planes shows evident fluctuations in the abundance of *Olenus* and *Homagnostus*; they co-occur rarely but are otherwise mutually exclusive, suggesting somewhat different requirements.

Ontogenetic development in Late Devonian phacopids.

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Phacopid ontogeny remains poorly known. Hitherto, only a few isolated pieces from the larval period (meraspis) belonging to Phacops and a growth series from the meraspis to the early holaspis period of *Trimerocephalus* have been published. Moreover, although discontinuity in post-embryonic growth for the meraspis period was established by intermittent changes in size and shape, a discontinuous developmental pattern for early holaspis instars which are not morphologically distinguishable from each other has never been unequivocally demonstrated. An opportunity for accurately tracing detailed growth patterns of a phacopine species arose from an exceptionally well preserved assemblage of silicified meraspis to early holaspis exuvia of *Trimerocephalus lelievrei* from a Late Devonian limestone nodule from Khorb-el-Atil near Erfoud (SE Morocco). In this study, a size analysis has enabled the size distribution of isolated sclerites of *Trimerocephalus lelievrei* to be established and the number of ontogenetic instars present in the fossil population to be determined. A morphometric approach based on outline analysis was then performed to quantify the shape changes among successive instars, as well as the allometry attached to the ontogeny of this species. First, the plurimodality of size distribution has allowed the recognition of several instars from the meraspis period to early holaspis period and provided definitive criteria to discriminate early holaspis instars. Shape study then permitted the demonstration of a progressive shape change during successive instars and also with size increase. The ontogeny of *Trimerocephalus lelievrei* is characterised by a shift from elaboration of shape during the meraspis period to growth in size mainly during the holaspis period. Finally, this study has shown that the particular phacopine mode of moulting, which involves the opening of the neck joint after ankylosis of the facial sutures occurred between the two first holaspis instars in *Trimerocephalus lelievrei*, whereas in ancestral phacopine ontogenetic trajectories, these sutures became ankylosed prior to the end of the meraspis period. This delay in the onset of ankylosis emphasises the importance of heterochrony in Late Devonian phacopine evolution.

Comparative paleoecology of Cambrian trilobite extinctions.

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In the Late Cambrian of North America, trilobite extinction events occurred at an average interval of about 5 million years. Consequently, there is an unparalleled opportunity for comparative studies of the dynamics of diversity change. Here, we present a comparison of biofacies patterns associated with the extinctions at the close of the Late Cambrian Marjuman, Steptoean and Sunwaptan stages (= Marjumiid, Pterocephaliid and Ptychaspid "biomeres") in Laurentian North America, based both on new collections and data compiled from the literature. All three events involve a profound reduction in both within-habitat (alpha) and between-habitat (beta) diversity. During and immediately after the extinctions, biofacies structure collapsed, producing an ecologically homogenous shelf with a small number of widely-distributed biofacies dominated by a few eurytopic trilobite taxa. The extinction intervals are characterized by rapid biofacies replacements and reduction in alpha diversity. These biofacies replacements reflect both extinctions of dominant genera together with extensive immigration of taxa from shelf margin and, especially off-shelf sites. Low levels of alpha and beta diversity persist for some time following the extinction interval. Such a lag is predicted by logistic models of diversification and is therefore not surprising. It could, however, be amplified by reduced speciation rates following the shift towards biofacies dominated by wide-ranging eurytopes. Previous analyses of Phanerozoic extinction patterns based on genera or higher taxa have viewed the Cambrian "biomeres" as minor events. However, the extent of ecological disruption of shelf habitats at each of the three Late Cambrian extinctions indicates that their severity has been underestimated. Moreover, recent work on the Permo-Triassic and Ordovician-Silurian events show that they are also characterized by shifts to low diversity, environmentally widespread biofacies. This suggests that the general ecologic characteristics of mass extinctions are not symptomatic of a particular forcing mechanism and, therefore, biofacies analysis may not offer a definitive test.

The ultrastructure of homalonotid trilobite cuticle.

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Trilobite cuticle in which fine microstructural detail is preserved is very rare. The latest suite of material we have investigated is that of an homalonotid from the Silurian of Sk ne, Sweden. The laminated outer layer reveals some novel structures and the nature of the original organic template for mineralization is deduced. Some ideas are formulated on the process of mineralization itself in the outer laminated and principal layers. A degree of organization is detected in the principal layer, but this may be secondary; the original nature of this layer remains enigmatic.

Phylogenetic relationships of trilobite-allied Arachnata.

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A monophyletic Trilobita ("Olenellida" + Eutrilobita) can be defined by presence of exoskeletal calcification and dorsal eyes with calcified lenses. The groups phylogenetically closest to the Trilobita are the Helmetiidae (Helmetia, Kuamaia, Rhombicalvaria), Tegopeltidae (Tegopelte, Saperion), and Naraoiidae (Naraoia, Liwia, Tariccoia, Soomaspis, Misszhouia). These four clades share uniquely derived characters, in particular their style of thoracic/pygidial tagmosis, indicating that they form a monophyletic group within the Arachnata. Some detailed characters present in these taxa, such as the division of the exopod into proximal and distal lobes (the former bearing lamellar setae and the latter fringed with bristles) and hinging of the exopod along the basis, are more generally distributed, also being present in xandarellids and other Cambrian forms, such as Emeraldella. The bilobate exopod appears to be very general within Arachnata (e.g., present in Sanctacaris). These appendage characters are, however, lacking in Agnostus. Evaluation of agnostid relationships should include all available evidence, without ad hoc dismissal of taxa or characters. Within the trilobite-allied clade, several features (including an anterior sternite and a notched anteromedian cephalic margin; drop-shaped ventral eyes set in an exoskeletal bulge) support the Helmetiidae and Tegopeltidae as sister taxa. Naraoiid monophyly is well-supported, forcing notions of a "nektaspid" grade as "soft-bodied trilobite" ancestors to be abandoned. The three-taxon statement (Naraoiidae)(Trilobita)(Helmetiidae + Tegopeltidae) remains unresolved, with different characters favouring each resolution: the style of hypostome attachment and edge-to-edge tergite articulation are shared by helmetiids and trilobites, whereas an ovate pre-hypostomal sternite that bears paired "frontal organs" is apparently unique to naraoiids, helmetiids, and tegopeltids. New data on larval appendages for Naraoia reveal major, possibly metamorphic, morphological changes in ontogeny that should be considered in determining character polarity in the the trilobite-allied arachnates.

Cladistic methods in biogeography: applications to palaeontology.

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Traditional palaeontological approaches to biogeography have either lacked an explicit phylogenetic component (e.g., using measures of overall similarity) or have been essentially narratives, tracking migrations up-tree through time. Cladistic biogeographic methods have as yet been largely unexplored by palaeobiologists - like cladistic practice in systematics, they offer our discipline analytical rigour and an expressly phylogenetic approach. The benefit is, however, reciprocal, because distribution data from extinct taxa can enhance hypotheses of area relationship based on living taxa. Fossils permit a degree of temporal precision that is unavailable for wholly extant associations, and allow novel biogeographic hypotheses to be formulated in the case of areas with complex (changing) history. The most widely adopted methods of cladistic biogeography are parsimony and component analysis. Methods that interpret internal nodes as ancestral distributions (e.g., BPA, geodispersal analysis, dispersal-vicariance analysis) conform to tree analysis whereas component analysis operates at the more general analytical level of cladograms. Basic assumptions, operations, strengths and weaknesses of these rival methods are illustrated by examples from Early Silurian trilobites. Three analytical problems complicate the conversion of taxonomic cladograms into area cladograms: taxa that occur in more than one area ("widespread taxa"), areas that lack representatives of one or more groups ("missing areas"), and areas that harbour more than one representative of a group ("redundant areas"). The trilobite examples demonstrate how different approaches to these three problems yield different area cladograms. Recommended procedures include not accepting widespread taxa as unambiguous indicators of area relationship, considering sampling practices in evaluating whether a missing area is due to primitive absence, extinction, or unsampled presence, and rescoring redundant areas as separate areas. General area cladograms should be based on simultaneous analysis of all relevant data rather than on the consensus of area cladograms from separate groups; this can be achieved by tree mapping (Page's version of component analysis) or by BPA.

Trilobites, Species, Higher Taxa--and the "Sloshing Bucket" Model of Evolution.

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Perusal of my 20-year old "Trilobites and Evolutionary Patterns" (Eldredge, 1978) reveals the absence of what I currently take to be the most fundamental--and significant--pattern of the fossil record: the "turnovers" (Vrba, 1985) of stable regional biotas ("coordinated stasis"--e.g. Brett and Baird, 1995). Two reasons underlie this absence: (1) the above cited papers had yet to be written--meaning the pattern itself had yet to be appreciated, and (2), perhaps more interestingly, such turnover patterns are inherently cross-genealogical, involving regional ecosystems rather than monophyletic groups. For good and obvious reasons, evolutionary biology focuses on monophyletic taxa. Yet turnovers of relatively stable biotas are emerging as the dominant motif in the history of life--which is surely relevant to notions of how the evolutionary process works. Brett and Baird (1995) discuss some 8 successive Appalachian stable faunas--in which, on average, 70-85% of species are present throughout the 5-7 million interval, and an average of only some 20% of species are known to survive the turnover event as components of the next succeeding stable biota. Though more rigorous analysis is necessary, it appears that most species are in stasis throughout the temporal intervals of such stable faunas. Vrba (1985) links turnover patterns to (1) ecologic-biogeographic factors (habitat tracking--migration out of, and immigration into, a region consequent on episodes of environmental change) and (2) true extinction and evolution--meaning speciation--both as consequences of disrupted habitats. Taken together, these patterns imply that adaptive change is concentrated in largest measure into speciation events--and that speciation events themselves are cross-genealogically bunched into relatively brief intervals of geologic time. Turnover events vary in magnitude--from local events involving relatively few species, to global mass extinction events involving the disappearance of larger taxa--both monophyletic (Trilobita at the end of the Paleozoic) and paraphyletic (birds survived while "dinosaurs" failed to at the end of the Mesozoic). [Extinction and evolution entail events at and below the "species level"--rendering paraphyletic taxa useful as referents especially for multi-species extinction events--but further compounding the dissonance between rigorous systematics and ecological-evolutionary theory]. In any case, it appears that radiations--and possibly origins--of taxa of higher rank are (arguably at least) "symmetrical": newly-extinct taxa are replaced (usually right away--after a lag that itself varies with the severity of the extinction event) by taxa of roughly the same rank. The classic example is the radiation of terrestrial mammals in the Middle Paleocene. Another is the (?)origin--and certainly radiation, of Scleractinia after the extinction of Rugosa (and other Paleozoic reefal block-components) at the Permo-Triassic boundary. How to explain such patterns? The dominant theme in evolutionary theory today is that competition for reproductive success (or even competition among genes for representation--Dawkins's (1975) "selfish gene" model) is both necessary and sufficient for evolution to occur. Yet, though I have claimed that population genetics ought to have predicted the ubiquity of stasis, it is clear that the cross-genealogical patterns of stability and turnover of regional (even global) biotas are wholly unpredictable and even explicable from such precepts--Dawkins's (1975) claims to the contrary notwithstanding. There is a clear alternative: one that accepts the hierarchical structure of both genealogical (evolutionary) biological systems (viz. genes, organisms, demes, species, higher taxa) and ecological systems (organisms, avatars, local ecosystems, regional ecosystems, world biota--"Gaia"). Evolution is the result of physical events disrupting ecosystems--the more pervasive the disruption, the greater the total evolutionary change. The greater the evolutionary change, the more different the rebuilt ecosystems--hence the "sloshing bucket" model of evolution. Where do higher taxa fit in? Predictions from this model are that (1) adaptive change--hence synapomorphies marking the very existence of higher taxa--need not be concentrated at major turnovers. Though adaptive change is in general tied up with speciation, and speciation with such turnovers, patterns of origination of higher taxa (defined as the earliest documented occurrence of that taxon's synapomorphy) is not expected to be positively correlated with degree of severity of the turnover. Mammals, in other words, had been in existence long before the Paleocene. In contrast, (2) episodes of proliferation of monophyletic skeins of species are predicted to be positively correlated with severity of turnover events. The task now is to take a well-defended cladogram of Trilobita to test these predictions.

Trilobite extinctions and recovery at the Late Devonian Kellwasser and Hangenberg crises.

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It is now well established that out of five Late Devonian trilobite orders three of them did not survive the end-Frasnian Kellwasser Event. Last representatives of six poorly diversified families (i.e. Harpetidae, Odontopleuridae, Styginidae, Aulacopleuridae, Tropicocoryphidae and Dalmanitidae) reached the base of the Upper Kellwasser horizon or its time-equivalent where they became extinct. Within the surviving Proetidae two subfamilies, the Cornuproetinae and Dechenellinae were already wiped out at the Lower Kellwasser pulse. Styginids disappear at that level in Europe but remained in Australia until the top of the Frasnian. Most of the latest Frasnian evolutionary lineages exhibit pedomorphic trends to eye-reduction and off-shore communities, prior to the extinction level, are all characterized by reduced-eyed or even blind forms. This is the case in all outer-shelf sequences where the oxygen depleted Kellwasser deposits are developed. In contrast mixed faunas of normally sighted and reduced-eyed forms occur in peri-reefal environments such as developed in the North-western Australian Canning Basin at that time. First post-event innovations occur among the solely surviving phacopids and proetids. The ancestry of many of these, such as that of Nephranops or of the Cyrtosymbolinae, is problematic and might be obscured by the effects of heterochrony. No surviving taxa of lower rank being known this absence of documentation might well be explained by the fact that exclusively off-shore biotas have been described so far. Neritic trilobites that might have survived in restricted shallow shoal areas, such as the Canning Basin, are currently being investigated. As in the uppermost Frasnian, world-wide deepening at the end of the Devonian was responsible to adaptive orthogenetic evolutionary trends to eye-reduction affecting outer shelf trilobite communities. These became fatally trapped by the sudden rise and spread of oceanic anoxia (Hangenberg Black Shale Event). At that time both endobenthic blind phacopids such as Dianops and the totality of the rather diversified sightless cyrtosymbolines vanished together with reduced-eyed epibenthic forms. In contrast, largely oculated proetids such as Waribole and Pseudowaribole from shallow platform habitats gave rise, in that environment, to descending lines that stood beyond the direct influences of the Hangenberg Event. In addition to those survivors that experienced a major radiation in the basal Carboniferous, the world-wide post-event eustatic shallowing brought about exclusively normally oculated Lazarus taxa such as Pudoproetus and Brachymetopus. These had evolved, with only minor morphological change, from mid-Devonian ancestral rootstocks, that were restricted, consequent to the mid-Givetian Taghanic onlap, to shallow refugia in which they remained in a very small number. Surprisingly, shallow water phacopids such as Omegops disappeared at the same time as all other deep-water phacopids being probable victims of their poor diversification.

Phylogenetic concepts in the history of trilobite classification.

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Trilobite classification systems have been claimed as 'natural' at least since the time of Salter (1864). Different authors have pursued their individual meanings of 'natural', although most have claimed that their classifications also reflect phylogeny. Two approaches to phylogenetics are representative: the tree-based, or stratigraphic approach, and the key-character approach respectively. The former is exemplified particularly by Cambrian specialists such as Franco Rasetti; the intention is to reproduce the actual tree of descent by means of stratigraphic and evolutionary series of species - the classification is imposed after the reconstruction of the tree. The key character approach identifies characters which are considered to be reliable indicators of descent - synapomorphies in modern understanding. Both approaches seek to identify confusing examples of convergence (multiple homoplasies). These convergencies were probably a response to repeatedly adopted modes of life, although there are few morphotypes corresponding with plausible life scenarios. As an example, I shall consider the effectiveness of the stratigraphic approach versus the character-based approach in resolving the classification and relationships of those trilobites with highly secondarily specialised pelagic morphology. Although it is certainly parsimonious to assume that unusual characters have appeared only once, it will be shown that past assumptions about uniquely derived characters as a basis for classification have frequently been overturned by subsequent critical studies. It is possible that some of the characters currently employed as the basis for high level taxa will also be shown to be capable of multiple derivation. For example, ventral skeletal morphology shows that the mode of attachment of the hypostome may have been directly related to feeding habits - and hence a possible target for convergent evolution.

Trilobites and correlation of the base of the type Whiterockian (Middle Ordovician).

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The base of the Whiterock Series defines the base of the Middle Ordovician in North America, and marks a fundamental watershed in the taxonomic composition and biogeographic signature of trilobite and other fossil faunas. The Whiterockian has recently been claimed as the global standard for the Middle Ordovician. The shallow-water, Bathyrurid Biofacies trilobites from Zone L in the classical sections of Ibex, Utah, were described by the authors in 1996. The faunas from the type section at Whiterock Canyon have not hitherto been described. Bed-by-bed collecting in this, and the parastratotype section at Meiklejohn Peak, has yielded diverse faunas of generally different and deeper biofacies from those at Ibex. In the Hot Creek range there occurs at this horizon the first post-Tremadocian, olenid biofacies fauna described from the western US. The base of the Whiterockian was also a time of dramatic biofacies shifts in several sections, associated with a sequence boundary. Furthermore, detailed comparison at the species level indicates that the 'golden spike' at Whiterock Canyon is substantially younger than the notional 'basal' Whiterockian (the *Tripodus levis* / *Isograptus lunatus* horizon) in the Vinini Formation, Nevada, proposed as a global standard. The fine temporal/environmental calibration offered by the trilobites will help elucidate the complex extrinsic events which controlled the faunal revolution at the base of the Middle Ordovician.

New data on the fallotaspids and their bearing on olenelloid phylogeny.

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Plastic deformation in Moroccan fallotaspid specimens suggests that the cuticles of *Fallotaspis* underwent early dissolution. It may thus be assumed that the cuticle of *Fallotaspis* was less calcified or that the cuticular calcite was more unstable compared with other early trilobites. The frequency of cracks in larger fallotaspid sclerites depends directly on the size and morphology of the sclerite. Investigation of intergenal ridges, posterior ocular lines, and associated fractures indicates that the so-called "metaparian suture" ascribed to the fallotaspids does not exist and this type of "suture" is mimicked by cracks. The circumocular sutures in *Fallotaspis*, *Choubertella*, and *Daguinaspis* are frequently an initiation point of fractures that tend to align parallel to the major axes of the cephalon and resulting vectors of deformation. Dorsal compaction in larger specimens tends to create an artificial cranidium. On the other hand, poorly developed sutures can be observed in groups of trilobites that generally have sutures. This observation devalues the idea of the major significance of the facial suture for trilobite systematics and taxonomy. A protaspid larva of *Fallotaspis* was recently described for the first time. Its shape suggests a benthic mode of life. The meraspid cephalon of *Choubertella* indicates both a well developed intergenal spine and a genal spine that is reduced to a rudimentary structure in adult individuals. Early growth stages of olenelloids seem to share a distinct segmentation of the interocular cheeks, a feature that is generally accepted as an ancestral character. However, this character is also visible in fallotaspid trilobites. Traditional systematic arrangements for the olenelloid trilobites are based on the assumption that the facial suture reflects a valuable and ancestral state of development and that the lack of a dorsal facial suture proves a close phylogenetic relationship of the olenelloid trilobites. However, an apomorphic character that proves the olenelloids to be a monophyletic taxon (or "plesion") does not exist. The majority of authors have accepted the close relationship of fallotaspid and olenellid trilobites. It was suggested that peramorphosis can be identified as responsible for a morphologic change of the cephalon from *Parafallotaspis* to *Olenellus*, and that the glabella of *Olenellus* can be derived by paedomorphosis from that of *Fallotaspis*-like trilobites. Although this explanation is generally sound, the gradient of change attests only to a general trend in the morphology of olenelloids. It has become apparent that the dorsal facial suture evolved several times from sutureless olenelloids, and the lack of dorsal sutures may not characterize a higher taxonomic group. We have to recognize at least nine facts that suggest significant differences between fallotaspid and olenellid trilobites and that olenellids and fallotaspids obviously are offshoots of separate early trilobite groups and represent separate higher taxonomic units. Redlichiids and ptychoparioids are most probably descendants of the fallotaspid stock, whereas holmiid and olenellid trilobites appear to represent branches of a separate lineage. An order Olenellida appears to represent a polyphyletic clade.

Revision of the genus *Onaraspis* Öpik 1968 and its biostratigraphic and biogeographic significance.

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The genus *Onaraspis* Öpik is an opisthoparian trilobite characterized by a marked genal spine inserted near the middle part of the cephalon lateral margin, a macropleural segment located in the posterior region of the thorax, and a relatively large subcircular pygidium. *Onaraspis* was originally discovered in Northern Territory and Western Australia by Öpik (1968) and in Southern Australia by Jell (1990). It was also noted in Israel (Jell, 1974) and, finally, forms close to *Onaraspis* were cited in Spain by Sdzuy (1971). Now, we report the presence of this genus in the Iberian Chains (Spain) and compare the Spanish specimens of *Onaraspis* with all previously cited. The present revision permits the assignment of the following species to *Onaraspis*: *O. somniurna* Öpik 1968, *O. adusta* Öpik 1968 and *O. rubra* Jell 1990 from Australia; *O. palmeri* (Parnes 1971) from Israel; and *O. altus* (Linñ & Gozalo 1986) from Spain. The species of this genus are closely related forms from a morphological and also from a biostratigraphical point of view. The Australian species occur in the Ordian Stage sensu Öpik (1968) and within the *Redlichia chinensis* biozone (cf. Bengtson et al., 1990). The Israeli species was dated as Issafenian (sensu Hupž, 1960) by Parnes (1971) and was also correlated with faunas of the Spanish Bilbilian Stage by Jell (1974); and finally, the Spanish species is recorded in levels from Bilbilian Stage (Linñ & Gozalo, 1986). Thus, we concluded that the *Onaraspis* species reported here are Bilbilian in age (latest Lower Cambrian), after the chronological scale proposed for the Mediterranean Subprovince (Sdzuy, 1971; Linñ et al., 1993). From a biogeographical point of view, the genus *Onaraspis* occurs in a band that extends from the Mediterranean region to Australia and represents the first polime-roid genus of trilobita that is shared by Spain and Australia during Bilbilian times. This suggests that there was some faunal connection between both marine platforms during Cambrian times.

Morphometric Approaches to Trilobite Paleobiology.

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Morphometrics and cladistics share a common advantage over traditional taxonomic approaches: They both require a consistent descriptive framework as the basis for comparison of form. In cladistics, the user must specify the state of each character, or make an explicit statement if a character state is unknown. In morphometrics permissible data can only be obtained from specimens with a complete set of the parameters under investigation, or for which an explicit procedure has been used to estimate missing values. Consequently, both methods encourage consistency and rigor in the study of morphology, and provide an ostensible basis for subsequent re-evaluation of results. This rigor facilitates the framing and testing of hypotheses about aspects of trilobite paleobiology. In this paper I present a review of morphometric techniques commonly applied to trilobites, and consider the kinds of research questions for which morphometrics provides particular insight. Most trilobite researchers have plotted histograms of character occurrence frequency, or have used bivariate plots to document specimen distribution within a morphological space defined by two linear measures. These plots assist in the discrimination of morphotypes, and/or illustrate aspects of ontogenetic or taphonomic variation. Traditional multivariate analyses, such as principal component analysis, build upon the bivariate approach by examining variation in multiple characters synoptically. Their main utility is the simplification of complex datasets, and in the discrimination of patterns of character covariation. Multivariate approaches are not inherently superior those based on fewer parameters, but they can help identify which bivariate or univariate relationships are likely to yield interesting information. Traditionally, the majority of morphometric information on trilobites has been in the form of a matrix of linear distances (e.g. length of glabella, width of pygidium, etc.), or on codings of presence/absence or multistate characters. In recent years techniques have been devised which either examine the outline shape of a structure (e.g. Fourier analysis) or which maintain information of the original geometric relationships between key morphological "landmarks" on the specimen. Landmark-based techniques provide powerful tools for the comparison of form because, within the Trilobita, homologies between landmarks can be inferred with confidence. A wide variety of statistical methods are now available to examine the relationships among these points. Morphometric approaches are particularly valuable for documenting patterns of variation within collections from individual localities, and for permitting comparisons between localities. Morphometrics can quantify the differences among morphologies, and can provide insight into the specifics of these differences, permitting interpretation of their likely causes. By providing a framework for assessing morphologic diversification, morphometrics allows patterns of evolution evident from taxonomic information to be contrasted with those based on form. This approach has yielded insights into constraints operative during trilobite evolutionary history. We can move on to place analysis of morphologic diversification within phylogenetic, environmental and temporal contexts, and to use morphometric information as data for phylogenetics.

Phylogenetic versus environmental control of segment production in trilobites: implications for the evolution of developmental programs.

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Two triggers have been invoked to explain why rapid evolutionary diversification took place during earliest Cambrian time. The intrinsic trigger suggests that developmental innovations evolved at that time which led directly to rapid diversification. The extrinsic trigger argues that changes in the external environment permitted rapid diversification of organisms whose developmental controls had evolved significantly before the base of the Cambrian. Paleontological data can be used to test these alternatives. Several primitive Cambrian trilobites show apparently lax regulatory control of post-cephalic segmentation, a pattern contrasting with that seen in later, phylogenetically advanced taxa, limiting their opportunity to speciate morphotypes with radically different bodyplans. In order to test this suggestion we examined patterns of segment development in an assemblage of middle Silurian trilobites from Lodenice, Czech Republic. The assemblage contained 11 common articulated trilobite species collected from a 2.4 meter stratigraphic interval at a single locality. Taphonomic evidence suggests that specimens accumulated on individual bedding planes in periods of days to months. Although collections came from several bedding planes all taxa likely experienced a similar degree of time-averaging and compaction-related deformation. Hence different species in the assemblage were normalized for taphonomic history. Variability in thoracic holaspid segment numbers was clearly demonstrated in the proetide *Aulacopleura konincki*, which is characterized by a multisegmented thorax. *Aulacopleura konincki*, unlike any other described trilobite, continued to add segments to the thorax throughout holaspid growth, and holaspid specimens had between 18 - 22 thoracic tergites. The odontopleuride *Odontopleura ovata* and *A. konincki* share a common early meraspid growth trajectory. While holaspids of *O. ovata* have cephalic lengths between 1.0 and 9.8 mm, all specimens show 9 thoracic segments. A similar pattern of constancy of holaspid thoracic segment numbers is seen in other common Lodenice trilobites, including the proetide *Scharyia wenlockia* (6 segments), cheirurid *Cheirus insignis* (11 segments), phacopid *Phacopidella glocheri* (11 segments), scutelluid *Planiscutellum planum* (10 segments), and lichide *Dicranopeltis scabra* (11 segments). These results suggest that segment variability at Lodenice is related to a particular morphotype, rather than to a general environmental cause that affected all trilobites in a similar manner. *Aulacopleura konincki* is an advanced proetide trilobite, but is convergent with primitive Cambrian morphotypes both in overall proportions and in its multisegmented thorax. Proetide sister taxa of *A. konincki* with fewer segments do not show marked segmental variability. The ability of an advanced multisegmented proetide to converge on a pattern of variation common among Cambrian trilobites refutes the notion of irreversible advanced developmental constraint on segment development. Rather environmental, as opposed to genetic, constraints appear to have determined patterns of intraspecific variation in holaspid thoracic segment numbers. Variation in segment numbers may have been tolerated in multisegmented forms, but critically disadvantageous in forms with fewer segments.

Numerical Approaches to the Analysis of Growth and Instar Development in Trilobites.

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In studying the biology of an organism it is important to understand the ontogenetic processes that it goes through as it develops into its adult morphology. The discontinuous nature of arthropod growth results in size distributions that are typically clustered into instar groupings, which have the important potential to allow growth to be described using relatively simple numerical models. Trilobites exhibit interesting developmental patterns with significant variation across the different groups. Some forms, like agnostoids, exhibit relatively simple, ostracode-like patterns of instar development, often with discreet instars. Other trilobites show similar patterns during early ontogeny, but their growth patterns become more complex later in their development. Finally, some forms appear to pass through transitions that act more or less like the metamorphoses that characterize growth in advanced crustaceans. We report on our research into developing quantitative methods for detecting, describing and modeling the instar growth of trilobites. Starting with a simple computer simulation of trilobite growth, we examined a series of methods available for mathematically detecting clusters of data points, representing instars. Since instar assignments are known from the simulations, we were able to analyze the ability of different techniques to accurately assign individual data points to their correct instar clusters. We did this after generating "trilobite growth series" following a variety of different models. We introduce a new method useful for assigning individuals to instars which involves fitting a simple harmonic function to histograms of values projected onto a Reduced Major Axis. We compare this method to that most often used, which is simple visual inspection, as well as to a series of other methods which may be useful, including various clustering approaches, a technique called quantum analysis, and other analyses. In addition, we discuss several potential metrics of "discreetness" that may be used to characterize whole populations, including mean nearest neighbor distances, and those based on mean distances from the average size of each instar (however this average size is determined). We use both the computer simulation, and published data for trilobite growth series to evaluate these methods. We also will discuss the effects of time-averaging and environmental variability on apparent instar discreetness.

The Role of Databases in Trilobite Paleontology.

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The topic of databases in trilobite paleontology is timely because confusion about databases is rampant, and new questions about databases--what to do with them and what to do about them--occur at every turn. Some paleontologists advocate the use of databases in sophisticated terms. Others wonder what the discussion is all about and how new ways of thinking about data will enhance the understanding of trilobites. Funding agencies demand that scientists develop databases without considering such questions as what constitutes a suitable database or how, why, and for whose use one should prepare a database. Meanwhile, questions of propriety, security, and compatibility loom and, far from being solved, are rarely addressed by anyone down in the data trenches. The dictionary defines a database as a usually large collection of data organized especially for rapid search and retrieval (as by a computer). The image that comes to mind when one hears the term database is an electronic, relational database designed for use by an unlimited array of end users with idiosyncratic goals. A database can also be viewed as simply a collection of related data. According to this definition, computers need not be involved; and the capacity for rapid retrieval is not a requirement. These two ways of describing databases contribute to the ambiguity in discussions about databases because, depending on the definition, any compilation of data can qualify. Databases vary along two continuous scales: a scale of interrelatedness of the data and a scale of generality of their application. On the scale of interrelatedness, a database can be as simple as a page of notes from a field book. No mechanism for retrieval of information exists, perhaps not even a table of contents. At the other end of the scale of interrelatedness lies the electronic, relational database in which all possible logical links among entities have been carefully modeled. The scale of generality measures the number of users, from one to many. Notes from a field book are typically used by only one or two people, but it is possible that such data could be widely disseminated. By the same token, one can imagine an electronic, relational database that is used by only one or two paleontologists. Such limited usage might stem from a special-purpose design, propriety, downright stinginess, broad lack of interest in the topic, or poor documentation. Increasingly, however, one expects such databases to be designed for use by many users. The future of databases in paleontology lies in the construction of electronic, relational databases irrespective of where they lie on the scale of generality. If the number of paleontologists continues to dwindle, an important aspect of the design of databases will be to capture accurate and precise data in a standardized format. The database-management system can then function as a repository for preservation of our paleontological heritage.

Epibionts on *Dicranurus* and some related genera.

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Reports of epibionts on fully articulated trilobites are uncommon in the literature. However, a carefully prepared sample of 14 articulated specimens of *Dicranurus hamatus elegantus* from the Lower Devonian Haragan Formation of Oklahoma has revealed encrusting organisms on 100% of the sample. The encrusting organisms are of 3 types: 1) fossilized hard parts of bryozoans, brachiopods, corals, crinoids, forams, and worm tubes; 2) endoliths of unknown origin that may represent algae and/or sponges; and 3) pyrite (now limonite) coating the spines, apparently formed from the decay of organic matter from an unknown encrusting organism. The epibionts are present on trilobites of different growth stages with an overall sagittal length ranging from 2.3 cm and 4.6 cm. Epibionts commonly encrust the genal, pleural and occipital spines and the cephalon. Encrustation may cover an entire pleural spine but not the pleural lobe itself. Occurrence of epibionts is less frequent on the thorax. Careful preparation has also revealed encrusting organisms on articulated specimens of *Dicranurus* cf. *D. monstrosus* from the Lower Devonian of Morocco, *Ceratonurus* sp. from the Lower Devonian of Oklahoma, on molted cranida of *D. hamatus* from the Lochkovian of New York, and on *D. monstrosus* from Bohemia, Czech Republic. Specimens of *Selenopeltis* encrusted by bryozoans and edrioasteroids have been illustrated from the Ordovician of Bohemia. These genera belong to the subfamily *Selenopeltinae*. Known articulated genera have pleural spines of variable length, a few of which are unusually long. This spine pattern contrasts with that of other odontopleurid subfamilies, and the elongate spines in *selenopeltines* may have a different function. The occurrence of epibionts on the spines of various species at different growth stages from different paleogeographic areas is unlikely to be coincidental. The attachment of epibionts on the long spines of the *Selenopeltinae* could have been advantageous by breaking up the outline of the trilobite making it less conspicuous to predators.

Relationship between Silurian trilobite extinctions and oceanic cyclicity.

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The evolution and extinction of Silurian trilobites may be correlated with the model of oceanic cyclicity and climatic fluctuation proposed by Lennart Jeppsson. This model is based primarily on carbon dioxide fluctuations between the atmosphere and ocean and attendant climatic and environmental factors. Jeppsson recognized two kinds of episodes and four kinds of events, the latter of which mark a stressful period of turnover between episodes. At least ten episodes and events occur during the Silurian, which Jeppsson related to conodont evolution and extinction. He determined that the Ireviken Event (late Llandovery-early Wenlock) affected the global conodont fauna (80% of the taxa became extinct) more profoundly than did all subsequent Silurian events. He also reported that Ramsköld found that half of the trilobite taxa became extinct on Gotland at this time. We believe that the Ireviken Event also marks the most significant extinction affecting Silurian trilobites in much of North America. Preliminary study of the trilobite faunas of the Upper Mississippi Valley, Great Lakes area, and Hudson Bay Lowlands shows a profound change in the dominant trilobite taxa at this time. Throughout this region, Llandovery carbonate rocks are characterized by an abundance and diversity of illaenids, such as *Stenopareia*. These trilobites are found in a wide range of environments, although they are most typical of reef and Benthic Assemblage 3 non-reef environments. In the early Wenlock, most illaenids disappeared abruptly and were replaced by morphologically similar bumastines (especially *Bumastus*), having parallel patterns of distribution, diversity, and abundance. (Only a single illaenid, "*Stenopareia*" ptercephalus, continued for a short time beyond this extinction event, co-occurring with bumastines.) In addition, several prominent scutelline genera (*Ekwanoscutellum*, *Meroperix*, *Opoa*) were replaced at this time by the scutelline *Kosovopeltis* and similar taxa. Likewise, phacopids, encrinurids, cheirurids and other taxa show similar patterns of change during the Ireviken Event. The appearance and disappearance of trilobite taxa throughout the rest of the Silurian suggest a correlation to Jeppsson's episodes and events as well. However, more precise biostratigraphic control of non-trilobite taxa and more precise ranges for trilobite taxa are needed to determine exact relationships.

The Erratencrinurus Group from Baltoscandian geschiebes (glacial erratic boulders).

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Geschiebes from the last three glacial periods that have been found in an area south of the Baltic Sea yielded fragments of the trilobite genus *Erratencrinurus*. A total of 18 species has been documented from Middle to late Upper Ordovician geschiebes, yet. Most of the species come from calcilutitic Baltic Limestones which belong to the Rakverian, Nabalian and Vormsian. Preparation of the *Erratencrinurus* fragments from these dense, micritic limestones is extremely difficult and thus rather time consuming. The *Erratencrinurus* group obviously branched off from *Encrinuroides uncatus* (Evitt & Tripp, 1997) in either the Lower Blackriveran, Lower Caradoc or Middle Viruan, which is confirmed by the characteristic hypostome of the *Encrinuroides* type. The *Erratencrinurus* group developed as an independent lineage in Baltoscandia with numerous species. The phylogenetic relationships between the latter are clearly traceable. A striking phenomenon is the great similarity between *Erratencrinurus seebachi* from the Rakverian and *Erratencrinurus vigilans* from the Bobcaygeon and Verulam Formation from South Ontario. *Erratencrinurus* is characterized by an ample, morphologically diverse tuberculation and the development of large paired spines at L3 and another big spine between L1 and L3. Three different kinds of a scutum rostrale have been observed on the yet documented species. The skeleton of most erratencrinurids are marked by pore canals in different positions. A new molt type comparable to *Paradoxides* has been observed on several exuviae of *E. seebachi*.

The Coding of Inapplicable Characters: Problems and Assumptions.

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In the coding of characters for phylogenetic analysis using current computer algorithms, there are several options to deal with characters that are inapplicable in certain taxa because the feature with which the character is associated is absent. Consider the marginal spines of the larvae of the three trilobite taxa A, B, and C: A has no marginal spines on the doublure; B has unbifid spines; and C has bifid spines. These morphologies can be coded using separate characters for the part and the character-variable: character 1 (marginal spines as the part: absent/present); and character 2 (shape as the character-variable: bifid/unbifid). Alternatively the part and character-variable can be fused into a single character (marginal spines: absent/unbifid/bifid). This second option is easily modified into a stepmatrix with differential weightings, whereby different weights can be given to each transformation. A third option is the coding of each observable feature as a separate character with absent and present character states: character 1 (marginal spines: absent/present); character 2 (unbifid spines: absent/present); and character 3 (bifid spines: absent/present). Each coding option is problematic. The first necessarily involves the use of "?"s, which current algorithms cannot distinguish from unknown data, for taxa in which a character is inapplicable. The second results in the potential loss of phylogenetic information. Although secondary recovery of this information can be achieved using either a stepmatrix or the ordering of character states, both of these modifications can be problematic because of their inherent assumptions. The third coding can produce meaningless combinations of ancestral states. Little attention has been paid to the assumptions associated with these various coding options. The choice of coding entails decisions on various assumptions: 1) whether spines are homologous; 2) whether spine and spine shape are at different hierarchical levels; 3) whether spine and spine shape are logically and phylogenetically dependent; and 4) whether one transformation has precedence over (is considered more likely than) another. Prior to choosing one of these coding options, one should determine whether the associated assumptions are acceptable or applicable to the analysis; errors will reduce the likelihood of correctly inferring the phylogenetic hierarchy. The eventual solution is the development of rules for new algorithms that are able to deal appropriately with inapplicable characters.

Garden City Formation Trilobite Larvae and Their Phylogenetic Implications.

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The Lower Ordovician Garden City Formation yields a considerable number of silicified trilobite larvae. Most of them are Phacopida (in particular, Cheirurina) and Proetida (mostly Hystricuridae). The larvae exhibit many morphologic features that are considered primitive among these groups. The described cheirurine trilobite larvae are *Tesselacauda depressa* (Pilekiidae), *Kawina sexapugia* (Cheiruridae, Sphaerexochinae), *Rossaspis pliomeris* (Pliomeridae, Protopliomeropsinae), and *Protopliomerella contracta* (Pliomeridae, Cybelopsinae). Morphologic comparisons suggest that there were at least three lineages of Cheirurina during the Early and Middle Ordovician; and each described species seems to represent a primitive member of each of these three lineages. The hierarchical relationships of the lineages are proposed as follows: lineage 1 = (*Tesselacauda depressa* (Cheirurinae (Acanthoparyphinae (two separate Sphaerexochinae groups)))); lineage 2 = (Protopliomeropsinae ("early" cybelines ("advanced" cybelines + Encrinurinae))). The Cybelopsinae constitutes lineage 3 which is considered a sister-group to the above two. Hystricurid larvae exhibit primitive features relative to younger Proetida and advanced features relative to Upper Cambrian Ptychopariida. These features strongly suggest that hystricurid trilobites be ranked as a family separated from the Solenopleuridae. Two distinct morphotypes (types 1 and 2) of hystricurid larvae are recognized. The type 2 morphotype is considered a phylogenetic intermediate between type 1 morphotype and larvae of the Ptychopariida, usually considered to include the ancestor of the Proetida. Four proetide larvae are also described: "Proetide A", *Goniophrys prima* (Telephinidae), *Licnocephala cavigliadius* (Bathyruridae), and *Pseudoclelandia* (Bathyruridae). The larvae of "Proetide A" display the most primitive features among known Garden City proetides, including the Hystricuridae. Larval features of *Goniophrys prima* (a telephinid) are different from those of younger telephinids, contradicting the proposed evolutionary hypothesis that this genus may be ancestral to younger telephinids. Larvae that show great resemblance to the styginids such as *Failleana* are found, suggesting that they may be the earliest representative of that group. The phylogenetic origin of the Proetida, from the Ptychopariida, is further corroborated by the existence of a phylogenetic intermediate, such as "Proetide A." In contrast, the origin of the Phacopida is still problematic; nonetheless, it should be noted that larvae of the Garden City pliomerids are very similar to earlier larvae of such ptychopariides as *Dunderbergia*. The Garden City trilobites are likely to give us further clues to solve the evolutionary origins of the Proetida and Phacopida, and help to unravel the "ptychopariid problem." The occurrence of several larvae from the formation, whose morphologies are similar to ptychopariide-type larvae, makes future research on these Lower Ordovician trilobites worth pursuing.

The Machari fauna: Middle to Late Cambrian trilobites from the Machari Formation, Yeongweol, Korea.

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The Machari Formation in Korea has been known to yield abundant and diverse trilobites of Middle to Late Cambrian age, which is called the Machari fauna. The formation consists predominantly of thin-bedded dark-gray to black dolomitic limestone and laminated black shale and measures ca. 200 m in thickness. The lower part comprises light-gray bioclastic grainstone, dark-gray shale and lime breccia. The bioclastic grainstone is composed mostly of skeletons of Middle Cambrian trilobites such as *Tonkinella*, *Olenoides*, *Kootenia*, and *Peronopsis*, whereas no fossils were found in the shale and lime breccia beds. The middle part is dominated by laminated dark-gray to black shale with occasional intercalations of thin dolomitic limestone beds and is extremely fossiliferous. The upper part is characterized by a conspicuous banded appearance formed by alternations of dolomitic limestone and shale beds, but is poorly fossiliferous. The biostratigraphic revision has been attempted for the middle part of the formation and subsequently eight Late Cambrian trilobite zones are proposed for the interval: i.e., *Glyptagnostus stolidotus*, *Glyptagnostus reticulatus*, *Proceratopyge tenue*, *Hancrania brevilimbata*, *Eugonocare longifrons*, *Eochuangia hana*, *Agnostotes orientalis*, *Pseudoyuepingia asaphoides* zones in ascending order. The oldest Late Cambrian zone so far recognized in the Machari Formation is *Glyptagnostus stolidotus* Zone which is succeeded immediately by *Glyptagnostus reticulatus* Zone. The close association of *Glyptagnostus stolidotus* and *Glyptagnostus reticulatus* zones provides a very accurate time horizon for intercontinental correlation of lower Upper Cambrian sequences. The superjacent 15-m-thick interval is designated as *Proceratopyge tenue* Zone, which is however poorly fossiliferous and shows a low diversity. The *Hancrania brevilimbata* Zone is dominated by the nominal species, but also contains *Stigmatocera coreanica*, *Innitagnostus inexpectans* and *Peratagnostus obsoletus*. The succeeding *Eugonocare longifrons* Zone comprises *Irvingella* sp., *Erinxanium similis* and *Kormagnostella minuta*, by which this zone can be correlated with trilobite zones of South China and Australia with considerable accuracy. The overlying *Eochuangia hana* and *Agnostotes orientalis* Zones comprise a number of short-lived trilobite taxa, apparently representing a period of rapid Late Cambrian trilobite diversification: the *Eochuangia hana* Zone comprises twenty-seven species, of which eighteen are confined to the zone and nine continue into the upper zone; and the *Agnostotes orientalis* Zone yields nineteen species with eight species restricted within the zone. On the other hand, the *Pseudoyuepingia asaphoides* Zone, the youngest trilobite zone recognized in the Machari Formation, shows contrasting faunal aspect from the lower two zones in containing several persistently-occurring taxa throughout the zone: they are *Pseudoyuepingia asaphoides*, *Proceratopyge gamaesilensis*, *Trilobagnostus hisakoshii*, *Pseudagnostus primus*, *Acmarachis hybrida* and *Peratagnostus orientalis*. This revised trilobite zonation of the Machari Formation provides an improved biostratigraphic framework for correlation with the Late Cambrian zones established elsewhere including South China, Tarim, Kazakhstan, Australia and North America.

Trilobite evolutionary relationships at the Superfamily level.

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A phylogenetic analysis of 52 trilobite superfamilies and families is undertaken using PAUP (Phylogenetic Analysis Using Parsimony), a computer program based on cladistic methodology. Data on 59 holaspid and protaspid characters was collected, although much was unavailable. Since the number of genealogical trees generated by PAUP was virtually limitless, certain decisions had to be made to make the data bank manageable. Lower Cambrian taxa (the Olenellids, Redlichiids Agnostids and Corynexochids) were run separately and a topology showing a good consistency was run as a backbone constraint in PAUP. A similar decision was made for the Phacopids, Asaphids and Odontopleurids/Lichids, three clades generally agreed to be monophyletic and whose interrelationships are fairly well understood: these were also grouped and used as a platen to simplify calculations in PAUP. One of the trees which showed a high consistency index and correlated well with existing stratigraphic information was chosen for analysis. The data supported the Agnostids and Eodiscids as a separate clade. The Redlichiids are thought to be paraphyletic and split into two megaclades, one stemming from the Paradoxidids and one from the Redlichiids. The Paradoxidids are closest ancestor to the Corynexochids, which are a much expanded group including the Emuelloidea and Ellipsocephaloidea, the Leiostegoidea and Dameselloidea and the Proetids. The Redlichiid clade is closely related to the Odontopleurid/Lichids through the Crepicephalids. These three groups are an outgroup to a second megaclade which includes three other sub-groups: the Solenopleurids/Norwoodiids & Nepeids, the Asaphids (including the Olenids, Marjumiids, Harpids and Trinucleids) and the Phacopids (including the Burlingiids, the Illaenids, the Holotrachelids and Ptychoparioidea). Missing data makes these results extremely tentative, and they should be viewed only as working hypotheses against which further data can be tested. No single character has yet proved to be taxonomically definitive. Dorsal sutures had the highest consistency index, but historically this feature has had only limited utility as all but proparian and secondarily marginal sutures are plesiomorphic. Hypostomal form had a fairly high consistency index but was not conclusive and conterminancy and natancy do not appear to be synapomorphic characters uniting monophyletic groups. Glabellar form and protaspid bauplan are other useful characters for the traditional grouping of Redlichiids and Ptychopariids (glabellar form), and Asaphids (protaspid form). The search for evolutionary relationships should continue with a more complete data matrix - especially ventral and protaspid/meraspid characters - at a lower taxonomic (family) level, with additional characters like eye size, size of pre-glabellar field, glabellar furrow form, etc. charted in detail.

What is Unique about the Cambrian Radiation? a Probabilistic Analysis.

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Cladistic analyses were used to reconstruct patterns of evolution for the trilobite superfamily Olenelloidea, an important component of Early Cambrian diversity. Cladistic analyses make it possible to place studies of tempo and mode of evolution into a rigorous hypothesis testing framework. Added to the cladistic data was information about the first appearance of lineages and their geographic distribution. This allowed two analyses. One considered the magnitude of speciation rates during the radiation. Previous analyses of diversification during the Cambrian have focused on higher taxonomic categories and a para- or even polyphyletic assemblage of organisms. Thus, the validity of these studies as an accurate gauge of the Radiation is questionable. When speciation rates are calculated for a monophyletic Olenelloidea they were found to be quite high in the earliest part of the Early Cambrian, at least when compared to rates of speciation in other invertebrate groups from later in the Paleozoic. However, speciation rates lag significantly behind those seen in Plio-Pleistocene mammals undergoing Turnover-Pulse, and also behind those of equine lineages in the early radiation of horses. Thus, while speciation rates were high in the earliest Early Cambrian, they were not phenomenally high, implying that high speciation rates in trilobites (an important part of the Radiation) are not an adequate reason for concluding that the rules of evolution during the Cambrian differed from those at subsequent time periods. Moreover, later in the Early Cambrian speciation rates decline to near typical levels. The second part of my study assessed the relative contribution of extrinsic, earth history factors versus intrinsic, organismic factors to the high rates of speciation during the Radiation. Biogeographic patterns in the olenelloids were analyzed using a modified version of Brooks Parsimony Analysis. These patterns indicated that the dominant mode of biogeographic differentiation in the Early Cambrian was vicariance, with little evidence for repeated episodes of dispersal between distinct biogeographic regions (geo-dispersal) indicative of continental collision or multiple episodes of sea-level rise and fall. This is quite in contrast to mid-Paleozoic proetids which show frequent geo-dispersal. The plates that the olenelloid trilobites occupied (chiefly Laurentia, Siberia, and Baltica) were exclusively splitting apart during the Late Proterozoic and Early Cambrian. The fragmentation of plates would isolate biotas and increase opportunities for speciation, and thus produce elevated speciation rates relative to other times when geo-dispersal was common. This could be seen as providing an extrinsic fuel for the Radiation. However, there might also be factors intrinsic to Early Cambrian trilobites that reduced their propensity for dispersal relative to their mid-Paleozoic kin. Geographic ranges of trilobite species in the Early Cambrian are narrower than later in the Paleozoic, and this is evidence for an intrinsic contribution to the Radiation.

Using phylogenies to analyze the tempo of evolution.

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Analyses of fossil taxa have made important contributions to our understanding of evolutionary theory, for the fossil record is the one chronicle of life's history. One of the primary areas in which paleontology has contributed to evolutionary theory is in the study of evolutionary tempo. This includes both intraspecific change and rates of speciation. The latter shall be the focus of this talk. Although fossils have contributed to our understanding of how rates of evolution may vary through time, such analyses have typically suffered from two defects. First, higher taxonomic entities were used as proxies for speciating lineages, and second, the higher taxonomic categories utilized were often paraphyletic or even polyphyletic assemblages. Such assemblages do not accurately convey the underlying genealogical pattern of relatedness, and because evolution proceeds by common descent, they must convey highly inaccurate or spurious information about the pattern of evolution. Therefore, all analyses that have employed para- or polyphyletic higher taxa to quantify rates of speciation must be considered at best only a first approximation of such rates, and at worst, fundamentally flawed. Phylogenetic analysis offers a way to ameliorate some of the flaws that have accompanied past studies of evolutionary tempo in the fossil record. Phylogenetic analysis does not guarantee the correct or true pattern of evolution, but it at least places such pattern on a firmer footing, and makes the testing of such patterns explicit. A phylogeny can provide two types of information relevant to analyses of evolutionary tempo and speciation rates. First, it gives an indication of the sequence of evolutionary splitting. Second, in conjunction with information about the stratigraphic distribution of taxa, it tells the minimum time period by which lineages must have diverged. Once a phylogeny is available, and we have a handle on the sequence and timing of speciation events within a clade, we can analyze rates or probabilities of speciation. A series of deterministic and stochastic methods for analyzing such rates or probabilities exist. Deterministic methods include the exponential model. This allows direct calculation of rates of speciation, which can be compared with rates from different groups or at different times. Stochastic methods include the use of the maximum likelihood and Galton-Watson branching process approaches. These methods allow testing of hypotheses in a statistical framework. For instance, calculating what is the probability that so many species could have been produced in a specific interval of time based on some characteristic rate of speciation. Based on the results of such a test, one could perhaps conclude that it is extremely unlikely that so many species could have been produced in such a short time unless speciation rates varied significantly. The purpose of this talk is to present different aspects of both stochastic and deterministic approaches to analyses of speciation rate. This will thus be an overview of the types of techniques that can be brought to bear to analyze patterns of evolutionary tempo in the fossil record.

Trilobite biofacies associated with microbialitic bioherms from the Upper Cambrian Ore Hill Member of the Gatesburg Formation in south-central Pennsylvania.

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Data collected on trilobite faunas and lithofacies within the Ore Hill Limestone Member of the Gatesburg Formation in south-central Pennsylvania allow expansion of the geographic and temporal scope of biofacies analysis of Laurentian Upper Cambrian trilobites to include the central Appalachian region and the uppermost Steptoean Stage. The dominant lithofacies within the member consists of thinly bedded, moderately bioturbated lime mudstones with thick dolomitic laminae. Thin to medium interbeds of bioclastic lime grainstone (probable tempestites) provided most of the trilobite collections. These lithologies confirm a shallow subtidal environment of deposition below fair weather but above storm wave base. Faunas recovered in high-resolution sampling allow assignment of strata to, in ascending order, the *Pseudosaratogia magna* Fauna, the *Elvinia* Zone (with a lower *Cliffia lataegenae* Subzone and an overlying *Irvingella major* Subzone), and the *Taenicephalus* Zone. Analysis of Steptoean collections from this lithofacies, reveals a numerical dominance by the genera *Camaraspis*, *Cliffia*, *Deckera*, *Dellea*, *Drabia*, *Kindbladia*, and *Xenocheilos*. This suite of genera corresponds well with Westrop's (1986) *Xenocheilos-Kindbladia* Biofacies for the highest Steptoean Stage (pre-I. major Subzone) in Alberta. The Ore Hill occurrence of this biofacies confirms its presence on the southern margin of Laurentia in a somewhat shallower platform environment. A second lithofacies in the Ore Hill comprises meter-scale, microbialitic bioherms and associated lime grainstones. This lithofacies, which occurs at several levels within the member, yields faunas that represent different biofacies than those recovered from the dominant lithofacies. The oldest bioherms are thrombolitic and yielded trilobites of the *Pseudosaratogia magna* Fauna. The eponymous dokimocephalid genus numerically dominates the fauna within both the microbialitic lime boundstone and the associated lime grainstones. High in the *Cliffia lataegenae* Subzone, bioherms with a massive structureless microbialitic texture and associated inter-bioherm grainstones yielded a unique fauna numerically dominated by the catillicephalid genus *Buttsia*, foreshadowing the dominance of this family within younger Sunwaptan microbialitic bioherms (*Plethopeltid-catillicephalid* Biofacies of Ludvigsen and Westrop, 1983). The remainder of the fauna consists of *Pseudosaratogia* and five previously undescribed species of genera common in the dominant lithofacies. The youngest bioherms occur in the *Irvingella major* Subzone. These reefs, which exhibit a digitate structure and a structureless microbialitic fabric, yielded a fauna dominated by the dokimocephalid *Sulcocephalus candidus*. Coeval subtidal grainstones from Oklahoma and outer shelf shales from Alberta have yielded faunas characterized as the *Irvingella-Comanchia* Biofacies by Westrop (1986). The dominance of *Sulcocephalus* in the Ore Hill bioherms confirms slightly greater lithofacies-specific variation in the taxonomic content of I. major Subzone faunas than previously had been documented. These reefs also document that the extinction of *Buttsia* at the top of the Steptoean Stage brought about (at least in this area) a hiatus in catillicephalid abundance in microbialitic reef faunas in the lowest Sunwaptan.

Taxonomy and ontogeny of triarthrinid trilobites from the Middle Ordovician of Jämtland, central Sweden.

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Triarthrinid trilobites are widely distributed in the Middle Ordovician Andersön Shale and Örn Shale of Jämtland, central Sweden. These two formations consist predominantly of argillaceous rocks and they form part of the Lower Allochthon in the central Scandinavian Caledonides. The triarthrinids are represented by at least five species, belonging to two genera, *Porterfieldia* Cooper, 1953 and *Triarthrus* Green, 1832. *Porterfieldia* is represented by a single species, *Porterfieldia humilis* (Hadding, 1913), while at least four species belong to *Triarthrus*, the last olenid genus: *T. billingsi* (Linnarsson, 1875), *T. freji* Thorslund, 1940, *T. jemtlandicus* Linnarsson, 1875, and *T. linnarssoni* Thorslund, 1940. *Porterfieldia humilis* is only present in the lower Andersön Shale, equivalent to the *Hustedograptus teretiusculus* Zone. *Triarthrus freji*, *T. jemtlandicus* and *T. billingsi* occur frequently in the upper part of the Andersön Shale, which comprises the *Nemagraptus gracilis* Zone, and probably also the lower part of the *Diplograptus multidentis* Zone. *Triarthrus linnarssoni* occurs throughout the Örn Shale (mainly *Dicranograptus clingani* Zone). *Triarthrus jemtlandicus* and *T. aff. linnarssoni* are also sporadically present in the lower and middle part of the Örn Shale. Some mudstone beds in the Upper Andersön Shale are crowded with specimens of *T. billingsi* in almost all stages of growth, ranging from anaprotaspides to adult holaspides. These mudstones may represent a mass-mortality or collective moulting horizons. Protaspides and early meraspides are very rare, but those encountered are fairly well-preserved. The anaprotaspid is subcircular in outline and highly convex. The axis consists of five rounded, not clearly defined segments. The anaprotaspid has tubercles set in pairs on the dorsal surface. A pair of small slender spines projects forwards and outwards from the anterior margin. A pair of knobs is located on each side of the anterior part of the axis. The spines, tubercles and knobs are also present in early meraspid stages. The meraspid phase is quite extended and consists of many different stages. As the trilobite grows into an adult, the posterior part of the fixigenae becomes relatively large (tr.), and the frontal area of the cranium becomes broader (sag.). Thoracic segments of early meraspid stages have a tiny axial spine. When the segments increase in size, the spine decreases in size and is only present as a node on really large segments. Furthermore, as the segments become larger, the pleural tips change from rounded to angulate to spinose.

A morphometric study of the globally distributed trilobite *Carolinites genacinaca* Ross.

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It is widely accepted that the lower Ordovician trilobite *Carolinites Kobayashi* had an epipelagic mode of life. This interpretation is based on its functional morphology, analogy with modern pelagic crustaceans, and its geological occurrence. The palaeogeographical distribution of the genus is remarkable. It achieved its greatest range close to the lower-middle Ordovician boundary, with the species *C. genacinaca*. Occurrences of this species, or forms very similar to it, are reported from the western United States, Alberta, Argentina, eastern Greenland, Spitsbergen, the Baltic area, NE Russia, Kazakhstan, east central China, central Australia, southern France and southern Turkey. The distribution of the species was effectively global between, but not confined to, the palaeolatitudes of approximately 30°N and 30°S. Geometric morphometric techniques are being used to study intraspecific variation within *C. genacinaca*. The results have implications relating to the transmission of heritable variation throughout such a widespread population. This work forms a necessary starting point for a study focusing on the nature of evolution in *Carolinites*. It appears that the same stratigraphical sequence of species occurs in the lower to middle Ordovician throughout the palaeogeographical range of the genus, and characterizing the extent of variation on a single time plane will help in understanding this pattern.

Evolution, paleoecology, and taphonomy of trilobites in Silurian reefs of the central United States.

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Racine Dolomite reefs of the Great Lakes region contain one of the most widely recognized Silurian trilobite faunas in the United States. These reefs, ranging from early Wenlock through Ludlow in age, occur throughout northern Illinois and eastern Wisconsin. A similar fauna occurs in age-equivalent reefs in Iowa, Indiana, Ohio, Michigan, and southern Ontario. Trilobite diversity in Racine Dolomite reefs is among the highest known from the Silurian of the area, with some individual reefs containing more than 30 taxa. This diversity, however, does not represent a single living association, but comprises several distinct associations that represent different stages of reef development or distinct but contemporaneous reef environments. Diversity does not seem affected by reef size or age. The most prominent association occurs in the reef core and proximal flank, and is dominated in both diversity and abundance by bumastines, with some individual reefs containing five or more taxa. Lichids, scutelluines, odontopleurids, and cheirurids also characterize this association. Distal flanks contain an association that is transitional between reef and inter-reef trilobites. The inter-reef fauna, however, is truly distinct in taxonomic composition and dominance, being characterized by calymenids, dalmanitids, encrinurids, and phacopids. Taphonomic concentrations of trilobites are a conspicuous feature of Racine Dolomite reefs with the majority of specimens preserved in hydrodynamically-controlled accumulations of disarticulated molts associated with sediment traps. These accumulations falsely imply that trilobites were numerous when, in reality, they composed less than one percent of the entire reef biota. Three biogeographic zones are recognized in reefs of the region based on the mutually-exclusive distribution of bumastine genera and species and morphologically-similar genera of large lichids and scutelluines. Taxonomic stasis appears to characterize these reef faunas from their initial appearance in the early Wenlock (Waukesha Dolomite) through late Wenlock and Ludlow (Racine Dolomite). Older reefs are rare throughout North America; however, Llandovery reef trilobites are taxonomically distinct, although morphologically similar, to those in younger reefs. The abrupt disappearance of the Llandovery reef trilobite fauna and its replacement by the bumastine-dominated fauna can be correlated with the Ireviken Event of Jeppson's oceanic cyclicity model. All of these Silurian reef trilobite faunas are typical of an illaenid-styginid-lichid-cheirurid association, which dominated the trilobite component of all normal-marine reefs from the Ordovician through Devonian worldwide. This association is characterized by morphological stasis indicating that trilobite niche-partitioning was relatively stable for more than 100 million years. The late Ordovician extinction event appears to have had only minimal effect on this association as key taxa continued across this boundary on a generic level, and no evidence for a radiation in the reef environment exists. In contrast, Silurian reef trilobite faunas exhibit more significant change following Jeppson's Snipklint Episode (late Llandovery-early Wenlock) when illaenids were replaced by bumastines, and in the post-Ludlow (?Pridoli) extinction of the bumastines.

***Anomalocaris* predation on mineralized and non-mineralized trilobites from the Early Cambrian Emu Bay Shale, South Australia.**

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The giant Cambrian arthropod *Anomalocaris* has been cast as the villain in several cases of trilobite predation, based mainly on its size, the possession of presumed raptorial appendages and its unusual jaw structure. Pre-eminent is the unusual jaw morphology, seen as the only known coeval structure capable of inflicting characteristically arcuate-, wedge- or "W"-shaped bite marks exhibited by some trilobite fossils. However, doubt remains as to the durophagus abilities of *Anomalocaris*. Specifically, how could the jaw apparatus inflict such wounds on biomineralized skeletons, since the jaws, whilst stout, appear to have been poorly sclerotized, and the teeth could probably not occlude? Indeed it has been suggested that anomalocaridids preyed primarily on the abundant non-mineralized fauna. New insights into the predation method of *Anomalocaris* comes from the Early Cambrian (Botomian) Emu Bay Shale, which includes the mineralised and non-mineralised trilobites *Redlichia* and *Naraoia* and two species of *Anomalocaris*, with the first body fossil record of predation on non-mineralised organisms. A specimen of *Naraoia* exhibits a large, wedge-shaped bite mark on the right side. Opposite and slightly anterior of the bite mark, the left lateral margin also exhibits damage, being pinched inwards. This is interpreted as a 'holding scar' caused by one of the grasping appendages of *Anomalocaris*, where it held the specimen while delivering the bite. Examination of other fossils, similarly predated upon, confirms the presence of 'holding scars' in association with the bite mark. The configuration of the predation damage to *Naraoia* allows comparison with the structure and rheology of modern 'composite' arthropod cuticle, indicating that the appendages applied significant force and were thus actively involved in the post-capture predation process, rather than passively holding the prey. This process probably involved manipulation of the prey exoskeleton by the appendages, pivoting about a point where the jaws locked onto the organism. Such flexure would reverse the normal stress fields experienced by the layers of the cuticle, weakening them considerably. In this weakened state, pressure from the jaws would probably have been enough to fracture the mineralised cuticle, imparting a durophagus ability to *Anomalocaris*. Only one of the *Anomalocaris* species found in the Emu Bay Shale appears capable of such a predation strategy, suggests niche partitioning was already present within the anomalocaridids by the upper Early Cambrian. The possibility that a non-mineralised form such as *Anomalocaris* could practice durophagy has major implications for the importance of predation in the acquisition of mineralised exoskeletons and the escalation of predator/prey strategies. Especially considering that there is one defence against which this type of predation would be ineffective - enrollment.

Trilobite ecophenotypes: Examples from the Lower Ordovician of Baltica.

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Trilobite material comprising ca. 15.000 specimens has been sampled from the Komstad Limestone and Huk Formations of southern Scandinavia (Scania-Bornholm and Oslo region). These units are of late Arenig - earliest Llanvirn age (Volkhov-Kundan Stages, i.e. early Whiterock), and span five trilobite zones (Megistaspis polyphemus, M. simon, M. limbata, Asaphus expansus, A. "raniceps"). Several trilobite species, represented by several hundreds of specimens in the collection, exhibit a rather large morphological plasticity. Representatives of Nileus and Megistaspis serve to illustrate the range of variation. The exoskeleton of Megistaspis shows a total adult length:width range at the species level of about 30 or even 40 %, but in individual limestone beds the variation is usually only about 15 %. There is a systematic link between shallow water biofacies and narrow skeleton and deep water biofacies and broad skeleton, which possibly is a substrate relation, but in functional terms the variation remains unexplained. At the same time shallow water representatives of Megistaspis have a distinct cephalic posterior border furrow, a highly vaulted glabella, indistinct mesial impression in frontal area, and overall better defined ribs and furrows, in comparison with representatives from deeper water biofacies. The recurrent phenomena occur in several species and seems at least recognisable in two subgenera, and therefore the changeable morphology is interpreted as ecophenotypic rather than genetic (evolution). As the width of exoskeleton and especially the presence of a posterior border furrow on cephalon have been taken as important taxonomic features, this variation obviously entails huge problems for classification of the Baltoscandian Megistaspis group. However, the problem rather likely concerns asaphid trilobites in general. Species of Nileus show a quite uniform morphology and major importance has been attached to the external terrace line ornamentation for species distinction. For example the members of the N. depressus species group are characterized by a dense terrace line pattern on the pygidia (+/- the axis) and some subspecies even show terrace lines on the cephalon as well. However, this eye-catching feature systematically reflects the palaeoenvironment, and should be treated with caution in a taxonomical context. Different terrace line covered species/subspecies from Baltoscandia show the same trends of variation: representatives from deeper water palaeohabitats exhibit a moderately dense terrace line coverage of the pygidium and a smooth cephalic test. Approaching shallower water biofacies the pygidial terrace line density increases to almost twice as much, and eventually terrace lines spread onto the cephalon. Moving into still shallower water biofacies, all terrace lines are lost or almost so, and it is impossible to recognize the material as belonging to the N. depressus group. For nileid classification it seems more advisable to attach importance to cephalic structures and treat the external terrace line pattern with caution. The terrace line variation was previously thought to represent evolution and various so-called subspecies were considered valuable for correlation. However, the variation is recurrent and not contemporaneous in different regions. Similar variations are suspected to be present in several other trilobite groups (e.g. Illaenus, Raymondaspis), but large materials are needed to document the range of variation. An explanation of the 'plasticity' could be that the genetic control of phenotype in trilobites was less strict than in later crustaceans. The inherent taxonomic problems are immense.

Late Devonian progenetic proetid trilobites.

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The Famennian was a time of generally high sea-levels, following the extensive drowning of shallow platform seas during the 'Kellwasser Event' at the end of the Frasnian, when most major trilobite groups became extinct; only the Proetida and Phacopida survived. Of the former, several taxa appear to have undergone a pseudoextinction that embraced the later Devonian. These taxa reappeared at the very end of the period to diversify in the extensive platform seas which became reestablished following the eustatic sea level changes of the 'Hangenberg Event'. Famennian sediments of deeper water origin are dominated by proetids characterized by small sized individuals, with a preponderance of atheloptic (small-eyed and blind) taxa, especially in the upper part of the stage. These have been classified in various subfamilies, particularly the Cyrtosymbolinae and Drevermanniinae, and were formerly believed to have been ancestral to many, if not all the Carboniferous taxa. Feist (1995) demonstrated the effect of pedomorphosis on eye reduction and blindness in these trilobites, and their small size, combined with a reduced number of thoracic segments indicate that they arose progenetically, probably from an ancestor within the Proetinae, such as *Lacunoporaspis* or *Praedechenella*. Analysis of their morphological characters suggests that most belong to a monophyletic subfamily, the Cyrtosymbolinae, and that the Drevermanniinae is an artificial unit that was based on blindness as a unifying character. The Cyrtosymbolinae spread opportunistically following the 'Kellwasser Event', but became extinct, leaving no descendants, with the widespread regression that accompanied the initiation of the 'Hangenberg Event'. Other proetids that occur in association with the Cyrtosymbolinae in the Famennian are all early members of the Phillipsiidae, that probably have their origins in the Cornuproetinae. It is unlikely that late Frasnian *Palpberalia*, which shows progressive eye reduction and ultimately blindness was ancestral to any Famennian taxa; it probably arose independently from the Proetinae. *Cyrtosymbole* is the most primitive member of the subfamily, and shares cephalic and cranial characters with its presumed proetine ancestor. *Drevermannia* is similar to *Cyrtosymbole*, and is clearly related to it, but is blind. Two other groups appear to have been derived from *Cyrtosymbole* independently of one another, one centred on *Calybole*, the other on *Mirabole* and *Helioproetus*. The former is characterized by a narrow, pointed glabella with deep lateral furrows and a broad preglabellar field, and the latter by a flask-shaped glabella that reaches the anterior border. Both groups show repeated trends to eye reduction and blindness, and to effacement. *Cyrtosymbole* has a short preglabellar field, and was clearly libristomate. Both the *Calybole* and *Mirabole-Helioproetus* groups have brought the hypostoma into juxtaposition with the edge of the doublure, but in different ways. In the former the doublure extends inwards beyond the border, manifested as a prominent paradoublure line on the dorsal surface, whilst in the latter the preglabellar field has been eliminated by forward extension of the glabella. These modifications may have resulted through the independent adoption of similar feeding strategies.

Out like a lion: the extinction of the Olenellina and other related issues.

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One of the five richest localities for articulated olenellid trilobites on Laurentia occurs in the C-shale Member of the Pioche Formation in eastern Lincoln County, Nevada. The top of the 50cm-thick bed yielding this fauna marks the extinction of the Olenellina. This extinction event can be located within a few centimeters at several localities along a discontinuous 60km north-south outcrop belt. Six olenellid species, and species of *Crassifimbra*, *Zacanthopsis*, *Bathynotus* and *Oryctocephalites* constitute the trilobite fauna immediately preceding the extinction. Immediately above the extinction, one species, *Eoptychoparia piochensis* is abundant. There is no evidence for the decline of the Olenellina prior to the extinction event, and the diachronous contact of the C-shale Member with the underlying Combined Metals Member is transected by the event. This event is the oldest documented biomere boundary. The six co-occurring olenellid species, all represented by articulated individuals, have remarkably stable morphologies. They demonstrate the critical importance of knowledge of the whole exoskeleton for development of a robust species-level taxonomy within the Olenellina. They also show interspecific differences that suggest some rethinking of generic and subgeneric taxonomy in this group. Excellent silicified holaspid and meraspid material of several of these species from a nodular limestone interbed in the shale less than 2m below the extinction provides new ontogenetic information with the potential for further complicating olenellid taxonomy. Detailed stratigraphic control on two species of *Nephrolenellus*, represented by silicified material, provides data suggesting that in this instance a gradualistic scenario seems to dominate over punctuation. Inter-regional differences among the youngest olenellid assemblages in the southern Great Basin suggest yet-to-be-resolved micro-environmental preferences for some species.

Laurentia is ready for stages.

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The Cambrian of Laurentia can be divided into seven stages based on major changes in cratonic and shelf trilobite biotas. These stages can be assigned to three trilobite-based series, and a fourth pre-trilobite series if so desired. The general position of boundaries that are appropriately spaced stratigraphically, and are at or near continent-wide trilobite extinctions has been known for some time. Two of these extinctions have already been used to define the upper two stages. Details of stratotype boundaries for all of the stages need to be resolved, and the devil is in the details. However, the guiding principle is that Laurentian stages can be consistently defined and widely recognized by using major trilobite turnovers, mostly at extinction events, to mark their bases. Some flexibility is needed in recognizing the faunal criteria used to define the stage bases because the Cambrian does not always have the luxury of continent-wide distribution of species. Event biostratigraphy is an important component of the criteria. The time has come for Laurentians to bite the bullet and provide a succession of named stages that our colleagues elsewhere in the world can relate to when attempting intercontinental correlations.

Lower Ordovician (Billingenian) cheiruracean trilobites from the East Baltic.

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In the Lower Ordovician of Baltoscandia, cheiruracean trilobites are very rare. In Estonia and Ingria (St. Petersburg region of Russia), the oldest representatives of many taxa of this order appear in up to 0.5 m thick glauconitic sandstones of the MekĀla Member belonging to the *Megalaspides dalecarlicus* trilobite Biozone and the Billingen Stage. Until recently, the reported finds included 5 cranidia of a pilekiniid *Europeites lamanskii* (Schmidt, 1907), 4 cranidia and 2 hypostomae of a cheiruriid *Krattaspis viridatus* Öpik 1937 and one encrinuriid pygidium assigned to the genus *Krattaspis* by Balashova (1966). New material from this level in Estonia and Ingria collected by L.E. Popov (St. Petersburg) and the present author includes more than 100 specimens, assigned to the species *Europeites lamanskii* and *Krattaspis viridatus* and three new species from the genera *Encrinuroides*, *Cybele* and *Propliomera* n. gen. Abundant material from a thin clay layer in the middle part of the MekĀla Member from the Popovka outcrop in Ingria gives new information about the cephalon, pygidium and hypostome of *Europeites lamanskii*. This species was originally placed in the family Cheiruridae, then in the family Pliomeridae, but the concept of *Europeites* based on our new material is the closest to Pilekiidae. A new subfamily *Europeitiinae* includes pilekiid trilobites with a distinct anterior area of the fixed cheeks like *Sinoparapilekiinae*, but differing from those having glabellar furrows deepening inwards and meeting the deep axial furrow very faintly; abaxially widening posterior border with rounded genal angle; pygidium with two sharpering pleural spines directing upward from doublure. *Propliomera* n. gen. is very likely related to the genus *Pliomera* appearing in the upper part of the Lower Ordovician and *Pliomerops* and *Placoparia*, both appearing in the Middle Ordovician. According to the emended concept, based on the new material, *Krattaspis viridatus* shows the closest resemblance to *Cyrtometopiniids*. The studied material includes the earliest representatives of *Encrinurinae* and *Cybelinae*, contributing with new data to the phylogeny of these subfamilies.

Significance of the trilobite genus *Hundwarella* in the Cambrian sequences of Tethys Himalaya.

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The fossiliferous Middle and early Late Cambrian in the Himalaya is known from the Tethyan successions of Spiti, Kashmir and in the Zankar area of Ladakh. In the Lesser Himalaya, only Lower Cambrian strata are reported so far. In the Himalayan Cambrian sequences, various species of the genus *Hundwarella* are known. The genus is one of the most important provincial elements of the Middle and early late Cambrian sequences and is widely distributed in the Himalayan region, but is not known outside the Asiatic region. *Hundwarella* is a most important faunal element for stratigraphic correlation of Middle and early Late Cambrian sequences of Asia. It is a vital stratigraphic indicator for the correlation of the Cambrian sequences of Spiti, Kashmir and Zankar Himalaya. It is the only polymeroid trilobite genus common to all Tethyan Himalayan regions during the Middle Cambrian and up to the early Late Cambrian in Spiti and Kashmir. The study of various species at different stratigraphic levels indicate a patterns of evolution and migration in different Cambrian basins. The different species show evolutionary gradation in successively younger forms. The fossils are obtained from folded argillaceous rocks which has resulted in tectonic deformation of the fossils. The distortion is largely unidirectional, resulting from elongation or shortening of the exoskeleton or de-shaping of the fossils. However, distortion does not affect, to any appreciable extent, the deepening or weakening of glabellar furrows. *Hundwarella* has a special significance within the Himalayan setting because it occurs in different sedimentary facies. The extent to which the genus may have crossed geographical boundaries cannot be assessed because its occurrence outside the Australo-Asian region is unknown.

Development of trilobite biofacial zonation in Cambrian basins of the Siberian Platform.

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Biotic zonation of the Siberian Platform Cambrian was caused by differentiation of depositional environments. They were initiated in the Vendian, formed in the Lower Cambrian and preserved in general outline during the entire Cambrian: the deep-water open basins occupying the E, NE and occasionally NW parts of the Siberian Platform; the inner shelf covering the central and SW Siberian Platform; the outer shelf separated the inner shelf and open basins and represented an external margin of carbonate platforms. The inner, outer shelves and basin slopes are characterized by specific trilobite assemblages (biofacies) during a rather long-term time interval. One or a few taxa generally of a high rank (family, superfamily or order) are distinguished in these assemblages depending on their quality, diversity, frequency and extent of distribution. The leading role of the lower-rank taxa (genus and species) is defined, as a rule, in comparison of contemporaneous environments exhibiting facies similarity. Open basin environments were indicated by miomeroids (Pagetiidae in the Early Cambrian and Agnostida in the Middle and Late Cambrian) and to a lesser extent by polymeroids (Fallotaspidoidea and Protolenidae in the Early Cambrian, Paradoxididae and Oryctocephalidae in the Middle Cambrian, Ceratopygidae, Olenidae and Asaphidae in the Late Cambrian). The outer shelf (mainly reef slope) habitat conditions were most favourable for Fallotaspidoidea, Protolenidae and Pagetiidae in the Early Cambrian, for Anomocaridae and to a lesser extent for Dorypygidae in the Middle Cambrian, for Plethopeltidae and Pterocephalidae in the Late Cambrian. In the Early Cambrian the inner shelf environments are distinguished by a frequent change of biofacies (macrobiofacies Jakutidae, biofacies Neoredlichiidae, Redlichiidae, Protolenidae, Pseudoeteraspis-Parapoliella, Namanoia). Family Asaphiscidae in the early Middle Cambrian, genus Markhaspis at the end of the Middle Cambrian and genus Kuraspis in the Late Cambrian became the index facial taxa in the inner shelf. Biotic development is a reflection of directed geographical, hydrodynamic and tectonic changes of paleobasins. Among them the eustatic sea-level fluctuations are of primary importance. The Cambrian trilobite biofacies replacement occurs on the Siberian Platform, as a rule, at the moments of the fluctuation sign reversal and a distinct change in the rate of sea level rise or fall. The Cambrian stage and series boundaries, being established on the Siberian Platform, frequently coincide with the boundaries of biofacies in stratigraphic succession related to sea level fluctuations. If these fluctuations were of gradual and restricted nature then these stratigraphic unit boundaries cannot be isochronous levels at a global scale. The known levels of intercontinental correlation (the boundaries of the Middle Cambrian *Triplagnostus gibbus* and *Tomagnostus fissus* Zones and the Late Cambrian *Glyptagnostus stolidotus* and *Glyptagnostus reticulatus* Zones) correspond to the moments of the transition from the high- to lowstand sea level on the Siberian Platform in the Cambrian and appear to serve as a high-rank boundary.

Candidate stratotype sections in western Hunan, China, for the Middle-Upper Cambrian boundary.

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Two thick, richly fossiliferous, continuous sections of the Huaqiao and Chefu formations have been measured and collected in western Hunan. Documentation of the trilobite taxonomy and biostratigraphy is in progress. When that work is completed, one of the two sections will likely be proposed as a formal candidate for the Middle-Upper Cambrian boundary stratotype. One section is near Wangcun in Yongshun County and the other is near Paibi in Huayuan County. Both sections are in the Jiangnan Slope Belt. The candidate sections are mostly composed of carbonate strata that contain abundant and diverse trilobite faunas ranging from the *Ptychagnostus atavus* Zone to the *Glyptagnostus reticulatus* Zone. Other desirable stratotype attributes of both sections include ease of access along paved highways and excellent exposures. Lithology of the Hunan sections is mostly argillaceous limestone with lesser dolomitic limestone. Formations in the Paibi section, which contain many medium- to thick-bedded limestone breccias of debris-flow origin, are interpreted to have been deposited in upper slope environments. Formations in the Wangcun section differ by having only rare debris beds, and are interpreted to represent lower slope environments. Approximately 100 agnostoid species, assigned to 36 genera, have been identified in more than 200 collections from the two sections. Numerous well-preserved specimens are facilitating taxonomic revisions. Most genera and many species have worldwide distributions that are expected to significantly improve the precision of stratigraphic correlation between continents. Although study of the polymeroid trilobites is less advanced, they are important in containing characteristic taxa of both the North China and the Southeast China faunal provinces. The Hunan sections are provisionally divided into 8 agnostoid zones and 4 agnostoid subzones. A separate polymeroid zonation will be defined later. In descending order, the preliminary agnostoid zonation includes:

Glyptagnostus reticulatus Zone *Glyptagnostus stolidotus* Zone Zone of *Ammagnostus* n. sp. *Linguagnostus papilio* Zone *Lejopyge laevigata* Zone *Goniagnostus fumicola* Subzone *Proagnostus bulbus* Subzone *Linguagnostus transversus* Subzone *Lejopyge armata* Subzone *Goniagnostus nathorsti* Zone *Ptychagnostus punctuosus* Zone *Ptychagnostus atavus* Zone. It is provisionally suggested that the Middle-Upper Cambrian boundary be defined by the first appearance of *Linguagnostus papilio*. The lowest observed occurrence of this species is near the base of the *Agnostus pisiformis* Zone in Europe.

Lower Ordovician (Arenig) Trilobites from SE Sardinia (Italy): palaeobiogeographical and structural implications.

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Recent investigations carried out in order to give a modern description of the 'Palaeophycus plumosus' remains (read *Phycodes circinatum*) figured by Testa (1924), from the 'San Vito Fm.' (Cambro-Ordovician SE Sardinia), revealed not only the usual reliability of ancient citations but also an unexpected biota mainly composed by trilobites, graptolites and less common *Hyalolitha*, pelecypods, gastropods and inarticulate brachiopods. Excepted the endemic medusoid *Ichnusa cocozzai* Debrenne & Naud 1981, and several ichnofossils, no macrofossils were known and only the geographically sparse occurrence of acritarchs suggested a Middle and Upper Cambrian age for the San Vito Fm. (Barca et al., 1982; 1989) up to Arenig for equivalent deposits from distinct tectonics units (e.g. Solanas Fm., cf. Di Milia et al., 1993 and ref.). The deposits of the San Vito Fm. have been assigned to distal turbidites (Barca & di Gregorio, 1980) and the investigated area mostly considered as Carboniferous flysch (Barca et al., 1997), even if the widespread occurrence of *Phycodes circinatum* strongly indicated an Early Ordovician age for a large portion of these neritic sequence. Ichnofossils (*Phycodes*, *Planolites* s.l., *Rusophycus*, *Dimorphychnus*, etc.) are abundant in close outcrops and some of them occasionally occurs in the trilobite beds. Graptolites are poorly preserved and concentrated in peculiar beds, among them, *Didymograptus* (*Expansograptus*) sp. and others didymograptids are under study. The asaphid dominated trilobite assemblage is characterised by the high proportion of *Asaphellus* sp. (112 over 141 specimens), few *Niobella* sp. and one pygidium of ?*Ogyginus* sp.; three specimens have been assigned to *Geragnostus*, two cranidia and five pygidia to *Taihungshania shui landeyranensis*; in addition, three tiny articulated specimens, ten poorly preserved cranidia and one pygidium of the raphiophorid *Ampyx* sp. (representing about 10% of the trilobite assemblage) have been collected. These trilobite-graptolite remains occur in a few meters dark-grey micaceous siltstones band within a thick sequence dominated by sandy deposits rich in biogenic and sedimentary structures. Preliminary results: 1) The occurrence of *Taihungshania* in SE Sardinia allows a more precise age-bracketing of the upper San Vito Fm. and assume a particular biogeographic significance. The genus is known only from Lower Arenig strata in Montagne Noire and Aquitania (S France), Arenig in eastern Taurus and southeastern Turkey (see Dean & Monod, 1990), Middle and Upper Arenig in Yunnan and Yangtze provinces from China. These findings reinforce the biogeographical relationships between the mentioned areas during lower Palaeozoic, yet established from Early Cambrian onward. 2) The didymograptid, the typical raphiophorid biofacies, and the *Cruziana* ichnofacies as well, are indicative of shelf deposition in low latitude of the Atlantic province. 3) Palaeontological and stratigraphical evidences indicates not only the general sedimentary break between the Arenig and Caradoc sequences in SE Sardinia ("Sarrabese phase"), as in agreement with data from many localities along the former Gondwanaland platform margin, but also the occurrence in the studied area of Mid-Silurian transgressive deposits directly overlain the San Vito Fm., or younger Ordovician volcanoclastics, without deposition of clearly Caradoc-Ashgill marine deposits, as in most sections in Montagne Noire and also in Turkey. However, due to the structural complications, this possible extended gap between Arenig and Silurian deposits need further investigations.

Broken Upper Cambrian trilobite exoskeletons: indicator of the ravages and extinction of a soft-bodied predator in deep water.

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The lower Rabbitkettle Formation of northwestern Canada is a monofacial Upper Cambrian unit of calcareous, argillaceous siltstone, fine-grained sandstone and argillaceous lime mudstone, with rare bioclastic grainstone. These rocks were deposited on a gentle slope below fair-weather wave base with no discernible fluctuation in water depth over the Marjuman and Steptoean interval. The trilobite fauna is a mixture of pandemic agnostoids and Laurentian polymeroids, including protaspides and meraspides. Individuals are disarticulated, non-abraded and mostly oriented convex-upward. Bioclasts are interpreted as in situ elements that reproduced on the Rabbitkettle slope. They were affected only by weak bottom currents and storm-induced turbulence. A major proportion of the larger (845 mm across) polymeroid cranidia and pygidia in the Marjuman part are broken; large thoracic segments are often broken at the axial furrow and some broken free cheeks occur, but effectively no broken agnostoids or hypostomes were observed. Breakage is not species-specific, although *Cedaria* and *Crepicephalus* sustained most of the damage because they are the most common larger taxa. Trilobites are not broken in Steptoean beds above the base of the *Glyptagnostus reticulatus* Zone. Physical breakage cannot be dismissed entirely, but most damage is interpreted to be due to size-selective predation-possibly through lethal blows similar to those delivered by some extant stomatopod crustaceans. A possible culprit may be an animal akin to *Yohoia* known from the Middle Cambrian Burgess Shale. The distribution of attacked trilobites serves as a proxy for the presence and disappearance of soft-bodied carnivores. In the Rabbitkettle, it suggests that Burgess Shale-type animals may have suffered Late Cambrian extinction at the Marjuman-Steptoean 'biomere' event when most trilobite species vanished.

Trilobite taphonomy of a Silurian reef: Attawapiskat Formation, northern Ontario.

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Silurian carbonate buildups have been subject to intense paleoecologic and sedimentologic analysis, and have played a critical role in the formulation of key concepts such as reef succession. Most studies have focused on reef-constructing organisms although some have dealt with associated reef-dwelling components, including trilobites, brachiopods and crinoids. Taphonomic work has generally been limited and, as with studies of younger buildups, has mostly considered framebuilders. However, existing data for Silurian reef trilobites point to complex hydrodynamic sorting of non-framework components and emphasize the need for taphonomic assessment of buildup environments. Here we document taphonomic patterns of trilobites from undolomitized, exhumed patch-reefs of the Silurian (Late Llandoveryan; Telychian) Attawapiskat Formation of northern Ontario. In this setting, trilobite sclerites are often conspicuous and locally abundant. A total of 18 species, including scutellines, illaenids, cheirurids, proetids, encrinurines, calymenids and rare lichids and odontopleurids occur in two intergrading associations. Most striking are "nests" consisting almost exclusively of pygidia of the large scutelline *Ekwanoscutellum ekwanensis* (Whiteaves) that often contain more than 50 sclerites. Orientation data for 400 pygidia in 19 "nests" indicate that virtually all are concave-up; axial azimuth and anterior/posterior orientations appear to be random. Size-frequency distributions typically cluster around a single large size class. These data are consistent with transport, sorting, and concentration in minimal flow regimes. The second association, characterized by a smaller scutelline and an illaenid (but essentially lacking *Ekwanoscutellum*), occurs most abundantly in brachiopod-rich bioclastic rudstones that apparently represent higher energy deposits. The data emphasize the taphonomic complexity of Silurian buildups and indicate that extensive sorting of skeletons is a significant source of bias in paleoecologic analysis of vagile components of reef biofacies.

Middle-Late Cambrian transition trilobites of Asian aspects in Southern France.

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A diversified trilobite association has been recovered from the limestone coquina bed of the basal Val d'Homs Formation of Ferrals-les-Montagne, Montagne Noire, southern France. Different taxa are provisionally assigned to Bergeronites, Prochuangia, Proceratopyge, Paracidaspis, "Stigmatia", "Pesaia", "Szeaspis", a lisaniid and an ammagnostoid. Whereas no North European or American elements are represented, the assemblage is closely related to faunas from South-Central China, Iran, Kazakhstan and Siberia. In comparing the variously interpreted range charts of related forms it is difficult to assess the precise age of the French fauna. It supercedes levels with the last mid-Cambrian Paradoxides that are already associated with Asian invaders such as Chelidonocephalus and Dorypyge. Whereas Bergeronites and Proceratopyge are reported from both latest Middle and Late Cambrian, the other taxa so far are known from early Late Cambrian strata; some of them such as Prochuangia, Proceratopyge and "Stigmatia" range up into the middle part of the Late Cambrian. As index agnostoids such as Leiopyge laevigata and Glyptagnostus stolidotus are lacking, our assemblage fits presumably into the intermediate time-slot that is characterized in South-Central China by the Paradamesops jimaensis - Cyclolorenzella tuma and Liostracina-Chatiana Assemblage-Zones at the Middle to Late Cambrian transition. A precise age will only become apparent when the systematic palaeontology and exact ranges of the taxa are further explored region by region. At first sight, the Ferrals fauna appears to represent a mixture of Middle and Late Cambrian trilobites from more than one biostratigraphical zone. Generic associations described elsewhere, such as the occurrence of Bergeronites and Prochuangia on the same pieces of rock, lack of intraclasts and authigenic minerals, suggest an absence of reworking and an autochthonous deposit. The fauna belongs to the subtropical, shallow carbonate platform, agnostid-poor biofacies that developed at that time also in Iran (Mila Formation) and South-Central China (Laochatian Formation of western Hunan and eastern Guizhou). According to these data, the Montagne Noire must have probably remained within the warm-water latitudinal belt at the beginning of the Late Cambrian, with the implication that formerly developed models of the high latitudinal position of this area should perhaps be revised.

Morphological integration and phenotypic variability in trilobites.

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Analysis of shape and size in trilobites has traditionally used linear measures and their patterns of variance and covariance. Landmark based morphometric techniques are able to analyze the same problems with the added advantages of 1) measurement of truly homologous characters, 2) limiting redundancies within the measured variables, 3) retention of information about the original form and 4) straightforward graphical interpretation of results. Analyses are relatively uncomplicated, within spreadsheet programs such as Excel and in existing programs specifically designed for the analysis of landmarks (many available as shareware through the SUNY Morphometrics site [<http://life.bio.sunysb.edu/morph/>] and other web sites). There are several ways of manipulating sets of landmark coordinates digitized from multiple specimens. Procrustes methods superimpose sets of landmarks using least-squares or resistant-fit algorithm, and can be extended to include shearing. Thin-plate spline techniques perform a mathematically rigorous deformation of specimens analogous to the deformation grids developed by D'Arcy Wentworth Thompson. The landmark configuration from one form is superimposed upon another landmark configuration and the deformation of landmarks is decomposed into a set of descriptors of shape change. Uniform (shearing) and non-uniform shape changes are distinguished and non-uniform shape change is divided into a hierarchy that describes global versus localized shape changes within the set of landmarks. Shaw's (1957) standard measurement scheme for non-agnostidean trilobites has been transformed into a standard set of landmarks that can be widely applied within the group. A simple size measure based on landmark coordinates is easily computed and has the added advantage of being uncorrelated with all aspects of shape. Changes in shape are analyzed through the comparison of a reference specimen (an early developmental stage, an 'average' of all specimens or some other arbitrary form, depending upon the nature of the question) and other specimens. Analyses can also be undertaken within an explicit phylogenetic framework. The magnitude and orientation (anterior/posterior, medial/lateral and the like) of shape change are readily determined. Shape changes can be localized to specific regions within the form of interest. Analysis of the middle Cambrian ptychoparioid *Eoptychoparia piochensis* shows complex patterns of character change through ontogeny. Multiple taxa have been analyzed concurrently in order to construct a multivariate morphospace for the analysis of macroevolutionary shape changes in Olenellids and Agnostids. Extensions of the technique have been used to assess levels of developmental constraint. The role of historical versus local factors in determining attributes of organisms will be assessed by placing them into a phylogenetic context.

Understanding the Search for Affinities: The History of Research on Trilobites from Antiquity to the 1820s.

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Before the early 1800s, the affinities of trilobites were uncertain and enigmatic. Early workers speculated that trilobites represented vertebrates, molluscs, or worms, as well as being arthropods. After the affinity of trilobites with arthropods was universally accepted, they were variously grouped with other known high-level arthropod taxa before recognition of their unique high taxonomic status in the early- to mid-1900s. The early Chinese were well aware of fossils in general, and the first documented mention of trilobites appears to be in a early 4th century A.D. dictionary commentary. Apart from a possible reference to trilobite-bearing concretions by Albertus Magnus in the 1260s, the earliest European literature on trilobites (including illustrations) was given by the Welshman Edward Lhwyd in 1698. Lhwyd was convinced that the complete asaphid he found was a vertebrate, and also concluded that none of the fossils he found represented once-living organisms. Many workers in the 1700s such as Leonhard Hermann, Johann Jacob Scheuchzer, Francis Brÿckmann, Johann Woltersdorff, Johann Lehmann, Jacob Klein, and Franz Zeno concluded that trilobites were mollusc shells. This was based upon the superficial similarity of inverted pygidia to bivalves or brachiopods (also considered to be molluscs). The great naturalist Pierre Latreille in the early 1800s revived the by-then outdated view that trilobites were molluscs by pointing out the lack of observed legs, and suggested an affinity with polyplacophoran molluscs (chitons). Another early view held that trilobites were worms. Magnus Bromell in 1729 postulated that the numerous agnostoids found in some Swedish Upper Cambrian rocks represented worms. This opinion resurfaced in 1819 by M'Murtrie when he described a Devonian phacopid from Kentucky. The early Swedish paleontologist Roberg in 1715 studied disarticulated trilobite pygidia, as well as articulated brachyuran decapods, and recognized the arthropod affinities of the trilobite sclerites. Roberg noted that both groups of fossils represented "crabs." Recognition of the affinities of trilobites with insects or the Articulata (the 1700s-era umbrella terms for arthropods) became more common among many European authors, especially in Britain, Sweden, and Germany. The opinions of LinnŽ (Linnaeus), Walch, and others in the mid- to late-1700s that trilobites represented fossil arthropods were generally followed. Apart from Latreille, these views were universally accepted by the time the great monographs of Goran Wahlenberg and Alexandre Brongniart appeared. The continuing search for affinities among fossil taxa is more intense today, particularly among problematic forms known principally from lagerstŠten. In the ongoing discussion over the affinities of taxa such as anomalocaridids, opabiniids, lobopods, nektaspids, agnostoids, and others, it is emphasized that an understanding of the history of research on the affinities of a now-familiar group such as the trilobites may help prevent premature conclusions based upon too few characters.

Upper Cambrian biomes and stages, two distinctly different and equally vital stratigraphic units.

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Periodic mass extinction of Laurentian trilobites in the Late Cambrian resulted in a natural packaging of widespread Upper Cambrian platform facies into large biostratigraphic units whose boundaries are marked by pronounced changes at the family level. Thus, as originally defined (Palmer, 1965; Longacre, 1970), biome boundaries coincided with zonal boundaries, specifically the bases of the Aphelaspis, Taenicephalus, and Missisquoia Zones. Subsequent lowering of biome boundaries (Palmer, 1979) by one subzone to coincide with highly correlatable mass extinction horizons (bases of the Coosella perplexa, Irvingella major, and Eureka apopsis Subzones) disrupted the phylogenetic coherence of biomes and ultimately led to the contention (Ludvigsen and Westrop, 1985) that biomes are redundant, being nothing more than stages. However, biomes are not stages. The mass extinction horizons serve well as effectively synchronous surfaces to define the tops of the Marjuman, Steptoean, and Sunwaptan Stages, but none marks the replacement of families characteristic of the underlying zones by a low diversity fauna dominated by an opportunistic olenid or "olenimorphic" genus. That transition is proposed here as the defining characteristic of a biome boundary. The base of the Pteroccephaliid Biome is returned to the base of the Aphelaspis Zone where the eponymous genus emerges as the dominant taxon, replacing Coosella perplexa, a crepicephalid species that dominates the subjacent C. perplexa Subzone. Similarly, the base of the overlying Ptychaspid Biome is again placed at the base of the Taenicephalus Zone where the "olenimorphic" genus Parabolinoidea replaces Irvingella and Sulcocephalus, elviniid genera that dominate the underlying Irvingella major Subzone. The comparable transition at the top of the Ptychaspid Biome, however, is not the base of the Missisquoia Zone, the original base of the overlying "Symphysurid Biome" (Stitt, 1983). The basal, Missisquoia depressa Subzone is dominated by Plethopeltis, a genus characteristic of the underlying Ptychaspid Biome. Accordingly, the top of this subzone is proposed as the biome boundary, marked by the disappearance of Plethopeltis and appearance of the olenid Apoplanias which dominates basal faunas of the overlying M. typicalis Subzone. No revision of the placement of the Marjuman, Steptoean, or Sunwaptan stadial boundaries is necessary. Each of these mass extinction horizons, the boundary between Stitt's (1975) "stage 3" and "stage 4" of a biome, records a major event that appears to have been synchronous across the entire Laurentian platform. Additionally, the extinctions at the base and top of the Sunwaptan also affected faunal groups other than trilobites, allowing these horizons to be traced beyond the geographic range of the Laurentian platform trilobites. In contrast, biome boundaries are poorly defined or unrecognizable in shelfbreak and off-platform facies. Also, there is evidence that they may be diachronous possibly reflecting earlier replacement of platform taxa in deeper environments. Regardless of their time-significance, these boundaries record major transitions in the evolutionary history of Laurentian platform trilobites, turnovers that compartmentalize platform facies into large-scale biostratigraphic units (biomes) independent of the North American chronostratigraphic framework.

The Lower to Middle Cambrian transition in the central Appalachian region.

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Recent sampling of Lower to Middle Cambrian formations in Pennsylvania and Maryland has expanded the information available on the continuity of sedimentation across the base of the Middle Cambrian in platform, shelfbreak, and basinal settings in the Pennsylvania depocenter. Closely spaced collections from above and below the base of the Elbrook Formation in the Great Valley in Maryland confirm that the sharp contact with the underlying Waynesboro Formation is unconformable, apparently the signature in a shallow platform setting of the widespread Hawke Bay Event of Palmer and James (1979). Characteristic species of the Glossopleura Zone occur in the basal beds of the Elbrook, immediately above Lower Cambrian Waynesboro shales that yield *Olenellus*. The Middle Cambrian *Plagiura-Poliella* and *Albertella* Zones are omitted by the unconformity. This gap is similar to that documented (Campbell, 1971) in the thin, upper member of the Kinzers Formation in the eastern part of the Conestoga Valley of southeastern Pennsylvania, a shaly, off-platform unit that accumulated under starved basin conditions. Conversely, isolated collections from a thick succession of shelfbreak facies (Kinzers and Ledger Formations) in the western part of the Conestoga Valley, southeastern Pennsylvania document the presence of *Polliella* and associated taxa, indicating that the succession there is more complete. Poor exposure, structural complexity, and a complex mosaic of lithofacies continue to limit efforts to document the vertical succession of faunas within these shelfbreak units. Nonetheless, new collections from several horizons within a stratigraphically expanded Kinzers Formation assign more than 500 meters of carbonate strata in that unit to the Lower Cambrian *Bonnia-Olenellus* Zone. Many of the species recovered are known from limestone conglomerates in the Quebec Allochthon but others are undescribed taxa. Although stratigraphic control on trilobite collections within the Kinzers in this area remains fairly coarse, it is already adequate to demonstrate the unreliability of a number of thin, siliciclastic-rich intervals that were used previously as "key beds" for local correlation. Parts of the overlying Ledger Formation, which represents shelf-edge carbonate sand shoals, escaped dolomitization and have provided the first trilobites yet recovered from that unit. The sparse fauna apparently represents the upper *Glossopleura* Zone or slightly younger intervals. Trilobites from the overlying Conestoga Limestone, a toe-of-slope deposit with abundant intercalations of black shale, establish that it contains strata assignable to the *Bolaspidella* Zone.

Trilobite behavior in the Silurian.

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The autecology of several trilobite species within the Rochester Shale (Silurian; Wenlock) of Ontario and New York were studied by combining distributional, morphologic, taphonomic and ichnologic approaches. Collections of arthropod trace fossils made within the Trimerus biofacies of the Rochester shale include *Cruziana*, *Rusophycus*, and *Diplichnites*. It is believed by many that trilobites produced the trace fossil *Cruziana* as a "feeding trace" and that *Rusophycus* represents a "resting trace". Examination of the trace morphologies reveals distinctive differences between them. *Cruziana* specimens, ranging from 7 to 25 mm in width, tend to be shallow, with bundled telopodite scratches and normally prominent genal spine drag marks. *Rusophycus* specimens range from 30 to 85 mm in width, show a different style of scratches, are normally deeper, and never have genal spine or pygidial spine impressions. Within this biofacies only two species of trilobite are present. *Dalmanites limulurus* (Phacopina; Dalmanitidae) is relatively broad and flat, has long genal spines and a pygidial spine, and ranges up to 45 mm in width. *Trimerus delphinocephalus* (Calymenina; Homalonotidae) is subcylindrical and streamlined, with no genal spines and can reach widths of over 80 mm. Thus *Cruziana* can be assigned as the shallow surface-mining feeding trace of *Dalmanites*, and *Rusophycus* as the deeper burrowing feeding trace of *Trimerus* with reasonable confidence within the confines of the *Trimerus* biofacies of the Rochester Shale. No evidence has been found indicating that these trilobites ever used the other's feeding strategy. *Diplichnites* also ranges up to very large sizes, and those trackways over 45 mm in width can with fair certainty be attributed to *Trimerus*. However any trilobite species could have made those of smaller size, as one would expect with a simple walking trace. Also found within the Rochester Shale is the large lichid *Arctinurus boltoni*. Its broad flat doublure and well-developed terrace ridges has been interpreted as a "snow-shoe-like" surface, with the trilobite resting directly on the sediment. The presence of numerous specimens of the small calcareous worm tube *Cornulites* on the doublure would suggest that this interpretation is false. Furthermore, the posterior orientation of the apertures of the *Cornulites* specimens suggests a rheophilic response to persistent water circulation patterns beneath the trilobite. Large specimens of *Arctinurus* also bear a large number of epibionts on their dorsal shield, including cyclostome bryozoa, brachiopods (*Stegerhynchus* and *Atrypa*), and *Cornulites*, indicating that its upper surface remained mud-free. The presence of several age classes for *Stegerhynchus* indicates that molting either stopped or slowed greatly once adult size was attained, and that these trilobites may have had fairly long life spans.

Variation in the eyes of Eophacops and Acaste (Phacopida, Trilobita) and its significance.

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Among the calcified compound eyes of trilobites, the most remarkable are the schizochroal eyes of the Suborder Phacopina. As well as representing an ancient visual system of probably unique kind, schizochroal eyes show patterns of variation in lens distribution which have figured in discussions of possible dimorphism and polymorphism in trilobites species, and have been used by some authors as taxonomic characters. *Eophacops musheni* is a common species in the British Wenlock, and variation in the lens pattern on the visual surface is described from about forty well preserved specimens. Such variation is most common dorsally, posteriorly and ventrally; variation anteriorly is rarer. Individual adult specimens typically have nineteen or twenty files of lenses, but the number present is not correlated with specimen size. Two cases are described of individuals with twenty files in the left eye and nineteen in the right. Comparable cases occur in *Acaste* also. Dimorphism in the visual surface of *A. downingiae* is doubtful. The new data on the variation of the visual surfaces of *E. musheni* and *A. inflata* allow Clarkson's (1975) developmental model to be extended. Dorsal variation in lens patterns implies a) that the initial length of the section of the generative zone actively producing lenses was variable and b) that lens emplacement was initiated at different times relative to the descent of the generative zone in different individuals. If development of a lens was controlled by the distance from adjacent lens centres, and given that lenses are round and that emplacement began in a single horizontal row, hexagonal close packing and the development of dorso-ventral files result automatically. Cubic close packing could be produced by modifying the spacing factor in successive horizontal rows. The number of dorso-ventral files of lenses and their relative height are controlled by the length of the active section of the generative zone and its pattern of growth. The existence of individuals with eyes differing in the number of files demonstrate that file number is a consequence of a developmental programme, rather than being under immediate genetic control. Variation in the timing of termination of lens emplacement accounts for the observed variation posteriorly and near the base of the visual surface.

Review of the Caradoc (Middle Ordovician) silicified trilobites faunas of Virginia, U.S.A.

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The stratigraphical units involved are the Lincolnshire Formation, lower Edinburg Formation (lower and upper Lantz Mills and Liberty Hall facies), Oranda Formation and lower Martinsburg Shale, extending from the *Nemagraptus gracilis* to the *Dicranograptus clingani* biozones. Whittington's (1959) lists of trilobite occurrences have been updated and supplemented by faunas from 23 other collections in the U.S. National Museum. Frequencies are recorded; locations of collections are noted on five maps. The upper Lincolnshire Formation fauna previously known only from one species is now known to consist of 27 taxa, two of which represent new subspecies. An on-shore fauna lacks raphiophorids, which are abundant in the offshore lower Edinburg deposits. We propose the term 'Raphiophorid biofacies' to distinguish this deeper water part of the succession. A similar situation exists in the Girvan district, south-west Scotland, with which comparisons are made.

Quantification of compaction-related deformation on the degree of observed variation in fossils: taphonomic overprint in the trilobite *Olenellus (Olenellus) gilberti* Meek.

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The observed variation within fossil species is the combination of biological variation and taphonomically induced variation. By comparing the deviation away from particular idealized ontogenetic growth trajectories of morphological landmarks between specimens preserved in uncompact and compacted states, it is possible to quantify the degree of observed variation in position of these landmarks which can be attributed to compactional deformation. Using uncompact (silicified) and flattened (non-silicified) samples of the Early Cambrian trilobite *Olenellus (Olenellus) gilberti* Meek from the Pioche Shale of eastern Nevada, the idealized growth trajectories of 26 selected cephalic landmarks are found to be fairly linear during the growth stages represented, and preliminary analyses suggest that the degree of apparent variability in landmark position can be increased by over 100% due to compaction. Most compaction-related morphological change is concentrated around the glabella region due to folding of the proximal cheek areas over the lateral flanks of the glabella, which preferentially collapses due to its domed shape into the cavity between itself and the hypostome. Recognition and quantification of the degree of this non-biological variation is vital if the true biological nature of the fossil organism is to be understood.

Cladistics, Diversity and Taxonomic Turnover.

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Estimates of taxonomic diversity through time have generally relied upon counts of genera or higher taxa from the literature and the inherent biases of this method have received much discussion. Cladistic analysis offers an alternative approach to tabulation of diversity through the calibration of cladograms against the stratigraphic record. This approach permits time of divergence of taxa to be estimated and may necessitate stratigraphic range extensions or even indicate the presence of ghost lineages: branches of evolutionary trees for which there is no direct stratigraphic record but whose presence is predicted by cladistic analysis. In this way, cladistic analyses can 'correct' stratigraphic ranges of species and allow a more accurate census of diversity to be made. Examples from Lower Paleozoic trilobites will be used to illustrate these concepts. Analyses of extinction events are also based commonly upon counts of higher taxa, particularly when conducted on a broad geographic scale. Inclusion of paraphyletic groups can inflate the magnitude of extinction because such artificial groups are simply defined by the absence of apomorphies of sister taxa. Disappearance of a paraphyletic group is merely taxonomic pseudoextinction if the apomorphic sister taxon is among the survivors of an event. Even if the apomorphic sister taxa are also among the casualties, inclusion of paraphyletic groups in the analysis exaggerates the extinction by, in effect, tabulating the same clades more than once. The trilobite extinctions at the close of the Late Cambrian Sunwaptan Stage (= 'Optychaspid Biome') provide an example of the impact of paraphyletic groups on patterns of clade-level extinctions. Early estimates suggested that all shelf trilobites were eliminated at this event but removal of paraphyletic groups indicates that less than half of trilobite families were extinguished.

Trilobites from the Early middle Cambrian Yebeiwan Formation, Tongren, Guizhou Province, China.

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Fourty-eight species assigned to twenty-four genera of trilobites are described from the type section of the Yebeiwan Formation in Tongren, Guizhou Province. The Yebeiwan Formation (new) is a facies equivalent of the Kaili Formation and is a 62 m thick unit of micritic and lamellar limestones. Four of the genera and twenty of species are new.

Phylogenetic analysis of ontogenetic shape transformations.

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Phylogenetic studies often rely heavily on shape characters. Typically these are expressed in qualitative terms. Quantification would seem to have obvious advantages. But those advantages cannot be realized unless the quantified features are conceptually suited to systematic studies. The variables obtained by traditional multivariate morphometrics are conceptually inappropriate for systematics. By definition, those variables are inherently phenetic—they are functions of phenetic distances among taxa. For example, Canonical Variates are defined to maximize phenetic dissimilarity among taxa relative to variability within taxa. In addition to this obvious disadvantage, the variables are problematic for another reason: they are specific to a particular analysis. Because the basis for comparison is a function of phenetic distances among taxa, any change in the sampling scheme will alter the basis of comparison. This last attribute of the variables greatly complicates comparative studies of ontogeny. That is because each ontogeny, being analyzed separately, exists in its own morphospace. There is no common space in which to compare ontogenetic allometries among species. The new geometric methods circumvent both these limitations. The geometric variables are solely defined in terms of homologous landmarks so phenetic distances do not enter into their definitions. Because the variables are not contaminated by phenetic distances, there is a common basis for all comparisons. This means we can use ontogenetic transformations as well as static shapes in phylogenetic studies. The partial warps are perhaps the most useful of the new geometric shape variables for systematic studies. These variables are a function of the spacing of landmarks in a single form known as the "reference" or "starting form." The partial warps are geometrically independent and describe features at progressively smaller spatial scales. For example, a partial warp at large spatial scale might describe an anteroposterior gradient that extends over the whole body, while a more localized partial warp might describe a change in proportions within the head. While geometrically independent, partial warps are often correlated in ontogeny and may also be correlated in phylogeny. Ontogenetic correlations can be analyzed using conventional biometric methods, such as regressions of shape variables on size or age. Phylogenetic correlations require different methods of analysis because they are analyzed in context of a phylogeny. One intriguing question is whether the ontogenetic correlations predict the phylogenetic correlations. Based on one empirical study, ontogenetic correlations are surprisingly poor predictors of phylogenetic correlations. While these new morphometric methods have numerous advantages over traditional methods they are still limited. The most important limitation is that morphometrics produces descriptors, not characters. Characters are evolutionary novelties and, as such, they are phylogenetic inferences. Even the most sophisticated methods cannot generate characters automatically. While we could tentatively equate morphometric variables with characters at the outset of a study, we should expect to revise those judgements in the course of further analysis. Such revisions are based on the same systematic reasoning and principles used in studies of qualitative data. It may be tempting to use special methods for quantitative data but the same systematic principles apply to all characters. Special methods designed specifically for quantitative data often lose sight of the meaning of systematic concepts. No method should be used if it would not make equal sense for qualitative data. That principle allows us to evaluate methods for coding, for testing character independence, and for tracing character evolution.
