ODONTOPLEURA (TRILOBITA, SILURIAN), AND A METHOD OF CONSTRAINED CONGRUENCY ANALYSIS

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ABSTRACT—Odontopleura (Odontopleura) arctica, a new species of odontopleurine trilobite, is described from the Canadian Arctic. A method of cladistic analysis is detailed. Parsimony analysis should be performed treating all characters as unordered. The universe of directed trees implied by the resulting rootless network(s) can then be examined and a preferred tree selected by a criterion of congruency. Namely, the most parsimonious directed tree that accommodates the most congruent arrangement of character-states should be taken as the preferred cladogram. Since this is essentially a general congruency method operating within the constraints of parsimony, it is termed "constrained congruency." The method is applied to the genus Odontopleura, resulting in the recognition of two major species groups, the nominate subgenus and Sinespinapis n. subgen. Odontopleura (Ivanopleura) duffrenyi Barrande is tentatively included in the genus, but considered too poorly known for cladistic analysis. Species assigned to Odontopleura (Odontopleura) include Odontopleura ovata Emmrich, Odontopleura brevigena Chatterton and Perry, Odontopleura (Odontopleura) arctica n. sp., and Diaconanthaspis serotina Apollonov. Species assigned to Sinespinapis n. subgen. include Tanaassaspis llandoveriyanus Snajdr, Odontopleura greenwoodi Chatterton and Perry, Odontopleura macallani Chatterton and Perry, and Odontopleura nehedensis Chatterton and Perry. Odontopleura bombini Chatterton and Perry is tentatively placed in synonymy with Odontopleura nehedensis. The genus had a wide distribution throughout the Early and Middle Silurian, due to preferences for deep-water, distal shelf or shelf-slope transition zone habitats.

INTRODUCTION

This work describes a new odontopleurine trilobite, Odontopleura (Odontopleura) arctica n. sp., from the Canadian Arctic Archipelago. The six available specimens were collected in 1953 by R. Thorsteinsson from the Marshall Peninsula (lat 75°26'N; long 96°05'W) on the northwest coast of Cornwallis Island (see Figure 1). The specimens occur on a single slab of argillaceous limestone, most often as external or internal molds, but in one case with the exoskeleton preserved. The sample is a glacial erratic. According to Thorsteinsson's field notes (T. E. Bolton, personal commun.), the lithology and matrix of the sample, together with its position in the glacial drift, suggest that it was derived from the Cape Phillips Formation and that its horizon was above the highest undoubted Ordovician graptolites and below the lowest undoubted Silurian graptolites. Very poorly preserved monograptid fragments do, however, occur on the sample, indicating a Silurian age. Hence, the block can reasonably be assigned to the lowermost Llandovery. The specimens are housed in the type collections of the Geological Survey of Canada (abbreviated GSC).

Previous work on Silurian trilobites from the Canadian Arctic includes Whittington (1961), Bolton (1965), Perry and Chatterton (1977), Chatterton and Perry (1979), and Thomas and Narbonne (1979). This paper represents the first Arctic record of the genus Odontopleura Emmrich. This taxon also occurs in the Canadian Northwest Territories (Chatterton and Perry, 1983), the Baltic region (Brunot, 1967; Schrank, 1969), Great Britain (Thomas, 1981), southwest Ireland (Siveter, 1989), the Carnic Alps (Gaertner, 1930), the Polish Holy Cross Mountains (Tomczykowa, 1957; see Brunot, 1968, p. 9), the southern Urals (Brunot, 1968, p. 9), Bohemia (Brunot, 1968; Snajdr, 1984b), and Kazakhstan (Apollonov, 1980). An attempt has been made to clarify the phylogenetic relationships of the species included in Odontopleura by means of unordered cladistic analysis. The resulting phylogeny clearly supports a distinction between two major species groups, recognized as the nominate subgenus and Sinespinapis n. subgen.

METHODOLOGY

The aim of this study is not to summarize the general procedures of and justifications for cladistic methodology (many such review articles exist; an excellent review and introduction to the literature from a paleontological viewpoint is provided by Schoch, 1986). However, the method of cladistic analysis adopted herein differs radically from the outgroup-based procedures familiar to most paleontologists. In addition, a particular ontology of the term "character" is advocated. Both of these areas require explication.

Characters.—When one has assembled and delimited the group of taxa to be analyzed, the procedure begins by the development

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of taxonomic characters. A character is not a discrete entity, but rather a basis for comparison between taxa (see Ghiselin, 1984; Colless, 1985a; Duarte Rodrigues, 1986, for discussion). Those aspects of taxa being compared are themselves not discrete objects ("parts": Colless, 1985a, p. 230), but rather descriptive statements about objects ("attributes": Colless, 1985a, p. 230). Therefore, with respect to a single (i.e., homologous) organismic "part" or "feature," one can group the study taxa into mutually exclusive classes according to their possession of an attribute of this part. An example from the present study will clarify the issue. Most odontopleurine trilobites have interior pygidial border spines, defined herein as those border spines lying between the major border spines. "Interior pygidial border spine" is the part. "Number of interior pygidial border spines" is the basis for comparison, or character. Therefore "2" and "4" (i.e., "has 2," "has 4," Colless, 1985a, p. 230) are the attributes, or character-states. Some of the implications of this ontology are discussed by Ghiselin (1984) and Duarte Rodrigues (1986).

It is emphasized here that characters are not inherent to the organisms we study. Characters are something we create by specifying a basis of comparison between attributes of homologous parts of those organisms. They are subjective, not objective, in nature. As Meacham (1984, p. 27) has put it: "The creation of a qualitative character [character, in this discussion] is a complex operation that requires a great deal of logical interpretation and intuition. Because synthesis and interpretation are so predominant in character construction, this process resembles an act of invention more than discovery."

Compatibility and parsimony.—Once each study taxon has been assigned to a particular character-state for each character, the task is to assess the best possible grouping of taxa, given that different groupings will likely be indicated by different characters. Many methods are currently advocated. One technique is character compatibility analysis, or clique methods (see Meacham, 1980, 1981, 1983, and references therein). These procedures generally seek to identify the largest possible set of congruent characters (i.e., those whose character-state groupings of the study taxa are in agreement). The noncongruent characters are then discarded, and relationships are resolved through application of parsimony to the remainder. As Farris (1983) has pointed out, use of such a technique involves assuming that if a character exhibits any homoplasy (incongruency) whatever, it must be homoplasious in all cases. As homoplasy increases in the data set, more and more characters are excluded and compatibility methods will explain an ever smaller subset of the original observations (Farris and Kluge, 1979; Farris, 1983). An alternative, favored here, is the use of a cladistic, or methodological, parsimony criterion according to the Wagner methods formalized by Kluge and Farris (1969), Farris (1970), and Farris et al. (1970). Cladistic parsimony holds simply that homoplasy should be minimized in tree construction. For a succinct dem-
onstration that this methodological criterion is independent of evolutionary assumptions, see Farris (1983). For an attempt to provide a formal justification for the criterion and discussion of the philosophical problems involved, see Sober (1983, 1985) and Felsenstein and Sober (1986).

Outgroups.—Cladistic parsimony analysis conventionally seeks a directed result. Direction is often derived through use of an outgroup criterion. In the most basic terms, this involves some type of comparison between the ingroup and what is assumed to be a related monophyletic group, by means of which the character-state for each character is specified. Ideally, one derives these ancestral character-states by reference to the sister-group of the ingroup. Maddison et al. (1984) have provided a rigorous treatment of this type of analysis. What bears emphasis here is that much of their discussion is concerned with cases in which relationships among the outgroups used are resolved. It has long been argued (e.g., Colless, 1967, 1969, 1985b) that analysis under these circumstances involves circular reasoning. One analyzes the ingroup by recourse to an already known higher level phylogeny. This phylogeny, however, can only have been derived by reference to some other prior knowledge (of a still higher level phylogeny), and so on in an infinite regress.

A second type of outgroup procedure escapes this charge of circularity by dispensing with the insistence that relationships among outgroups be known. In its most general invocation, this criterion holds that any group can be used as an outgroup for analysis, with those character-states that occur in both the outgroup and ingroup taken as primitive. Hence, the method will work equally well regardless of the choice of outgroup, with the obvious restriction that as the phylogenetic distance between outgroup and ingroup increases, homologues may become fewer in number, and the potential for homoplasy will increase. In effect, however, this type of analysis yields an assessment of ingroup relationships based upon the supposition that the chosen outgroup is in fact the monophyletic sister group of the ingroup. The opinion is often expressed (e.g., Michaux, 1989, p. 22) that use of multiple outgroups will improve the analysis. If we (somehow) have knowledge of the pattern of relationship between them, this may be true, according to the reasoning outlined by Maddison et al. (1984). However, if we accept that such knowledge cannot be acquired by analysis but must rather be asserted a priori, and choose instead this second, more general, outgroup criterion, multiple outgroups do not help at all. When the outgroup is changed, a new, different hypothesis of sister-group relationship is in effect formulated. The central parameter of the analysis, that determining polarity, has been altered. No consensus can be derived among the resulting phylogenies. They have fundamentally different parametric bases and are not comparable. Support for each reduces to reexamination of the criteria by which the outgroup in question was selected. Hence, under this more general invocation of the outgroup criterion, additional outgroups simply compound uncertainty.

From an operational viewpoint, the outgroup criterion is sometimes difficult to invoke. Often, for a variety of reasons, no prospective outgroup may be apparent. Indeed, in the case of many extinct groups, higher level relationships are completely obscure, and the outgroup criterion cannot be applied. All of this is not to say that outgroups have no utility. In some cases, there may be a mass of corroborative circumstantial evidence supporting a sister-group relationship, just as in some cases there may be a body of physical evidence supporting claims by stratigraphic paleontologists of direct ancestry in their fossil sequences. As long as the assumptions involved are made explicit, outgroup analysis may provide useful insights about ingroup relationships. The point we wish to stress is that outgroup analysis involves making a large and restrictive a priori assumption of ancestry, and does not have universal applicability.

Unordered analysis.—Meacham (1984, p. 27, figs. 1-3) has identified three types of cladistic characters. The character-states of unordered characters are not arranged in a transformation series. There are two types of ordered characters. The character-states of un directed characters are arranged in a transformation series, but the polarity of the series is not specified. The character-states of directed characters are arranged in a polarized transformation series.

Analysis using unordered characters is advocated here. Such analysis will determine the most parsimonious arrangement of taxa, given that any character-state may transform into any other (of the same character), and that reversals are possible. No ordering or direction restrictions are placed upon the data. Such restrictions amount to a priori assumptions about relationship. Rather, to use Meacham’s (1984) phrase, the characters should be allowed to speak for themselves.

However, in and of themselves, characters have nothing to say about direction. Undirected analysis results in an undirected tree, a minimum length Wagner Network. In order to generate a directed hierarchy, one must decide upon the position of a root. To accomplish this, some methodological assumption is necessary. One alternative is to apply the outgroup criterion. With a hypothetical ancestor in hand, one can either include it in the unordered analysis and place the root at the terminal node occupied by it, or use the procedure advocated by Lundberg (1972), in which the ancestor is excluded from the analysis, but used to root the Network by determining the position at which it achieves the most parsimonious fit. If outgroups are to be used, the second is clearly the less restrictive, most assumption-free, and most parsimonious (Farris, 1982) option. If not, what are the options for ingroup analysis?

Ontogeny.—Ontogenetic generality criteria may provide important and useful ways of producing ordered characters. Obviously, they require knowledge of development. To the extent that detailed knowledge of ontogenetic development is generally unavailable in paleontology, ontogenetic criteria are of limited application. Of course, to the extent that such information is available, for example in many tetrabranch taxa, these criteria are relevant and useful, and the reader is referred to Weston (1988) for a recent review.

Patterson’s method.—Patterson (1988) has suggested that what he terms “general congruence” is the best method of ingroup analysis. This is described (Patterson, 1988, p. 74) as “... demanding that the information within the character set dictates the polarity of characters.” This is the central theme of the present paper: the best initial idea of relationship, and the most assumption-free cladogram, is that derived solely from analysis of ingroup morphology.

Patterson (1988, p. 74) noted that for n study taxa, there are $2^n - (n + 2)$ possible “cladistically informative characters” (hereafter abbreviated CIC). A CIC is one that defines a subset of the study taxa. Here, any character-state in which two or more study taxa have membership corresponds to a CIC. For $n \geq 2$ study taxa, there are $\prod_{k=2}^{n} (2k - 3)$ fully resolved cladograms (Cavalli-Sforza and Edwards, 1967; Felsenstein, 1978). Patterson’s (1988) method is to examine all possible rooted cladograms for the study taxa, and to score them for the number of CICs that they accommodate. His favored cladogram is the highest scoring.

This method, however, may yield an unparsimonious result. If a CIC does not fit the highest scoring cladogram at some point
as a unique and unreversed synapomorphy—i.e., if it demonstrates some homoplasy—it is entirely ignored, and therefore assumed to be homoplastic in all occurrences. This is a form of compatibility analysis, as Patterson (1988, p. 77) readily admits. Compatibility analysis, as stated above, explains less data than cladistic parsimony as homoplasy in the data set increases.

Method employed.—Patterson’s (1988) goal, that the cladogram be derived solely from ingroup data, is endorsed. Rather than accommodating the most congruent arrangement of character-states possible, however, it is argued that the primary consideration should be that the preferred cladogram is as parsimonious as possible. Unordered analysis will result in one or a number of maximally parsimonious Wagner Networks. Congruency can then be used to select a preferred cladogram from the family of trees implied by these networks.

An important point here is that the tree chosen by congruency scoring all possible rootings of a given network (a network with \( n \) terminal nodes has \( 2n - 3 \) possible root positions) is equivalent to that derived by placing the root on the longest branch of that network (i.e., the branch across which the greatest number of character transformations are required), assuming branch lengths are unambiguous for the topology being considered. Hence, if analysis yields a single most parsimonious network, the preferred cladogram is immediately obvious, as it is that derived from a root positioned on the longest branch of that network. If there are multiple equally parsimonious networks, the competing candidates for the final cladogram are the longest branch rooting of each. These competing cladograms can then be congruency scored, and the highest scoring taken as the final cladogram. In the case of a tie, a consensus tree may be derived according to a variety of available techniques (see Kluge, 1989, for a summary).

Patterson (1988) used congruency to determine final tree topology. Here, tree topology is constrained by the criterion of parsimony. The preferred cladogram is that which accommodates the maximally congruent arrangement of character-states, given that its topology requires also the fewest possible number of character transformations. We therefore propose to refer to this method as “constrained congruency.”

Unordered analysis is inherently more likely to produce multiple equally parsimonious networks than ordered or directed techniques, since it imposes no restrictions upon the types of character transformations possible. Constrained congruency is a methodological criterion for deriving a limited number of directed trees from a larger number of undirected networks, by maximizing the number of unambiguous synapomorphies uniting taxa.

Finally, we note that although we prefer herein to treat all characters as unordered, and to select final cladograms by the criterion of constrained congruency, we do not deny that assumptions about ancestral states may often contribute important elements to a phylogenetic analysis. In our opinion, however, such assumptions should be made only when there is a strong and explicit reason to do so. Blanket hypotheses of pinniveness of the sort required by directed outgroup analysis are undesirable.

The constrained congruency method can be outlined as follows.

Step 1. Create a character matrix, assigning membership in character-states as described above.

Step 2. Run the data as an unordered analysis to obtain a rootless Wagner Network (or a number of equally parsimonious Wagner Networks) for the study taxa.

Step 3. If a single network is obtained, choose the tree obtained by rooting the network on its longest branch. If multiple networks are encountered, examine the longest branch rootings of each, and score for the number of unique synapomorphies accommodated. This is accomplished by examining each node, and scoring for the number of character-states that include all of the taxa encompassed by that node, and exclude all of the taxa not encompassed by that node (see Patterson, 1988).

Step 4. Choose the highest scoring cladogram. If multiple cladograms have an equally high score, the final cladogram can be derived by a variety of available consensus techniques (see Kluge, 1989).

### Table 1: Characters used in congruency analysis of Odontopleura

<table>
<thead>
<tr>
<th>Character</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td>3L glabellar lobe</td>
<td>absent; 1, defined ventrally only; 2, defined both ventrally and dorsally</td>
</tr>
<tr>
<td>Longitudinal furrow at posterior of 1L glabellar lobe</td>
<td>0, very shallow; 1L lobe confluent with median glabellar lobe; 1, deep, separating 1L from median glabellar lobe</td>
</tr>
<tr>
<td>Axial furrow at anterior of 1L glabellar lobe</td>
<td>0, very shallow; 1L lobe confluent with fixed cheek; 1, deep, separating 1L lobe from fixed cheek</td>
</tr>
<tr>
<td>Occipital lobe</td>
<td>0, absent; sometimes with ventral trace of furrow; 1, weakly defined; 2, strongly defined</td>
</tr>
<tr>
<td>Occipital furrow</td>
<td>0, deep; 1, shallow and broad; 2, indistinct</td>
</tr>
<tr>
<td>Transverse distance of eye from 1L glabellar lobe</td>
<td>0, subequal to width of 1L lobe; 1, greater than width of 1L lobe</td>
</tr>
</tbody>
</table>

### Analysis of Odontopleura

**Data.** The characters and character-states used to code for unordered analysis of Odontopleura are shown in Table 1. The sources consulted for coding are listed in Table 2. Table 3 gives the character matrix used in the analysis. Note that while **O.**
TABLE 2—Species and sources used in congruency analysis of Odontopleura.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sources</th>
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<tr>
<td>Odontopleura ovata</td>
<td>Emmrich, 1839</td>
</tr>
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<td>Breton (1967, Pl. 30, fig. 1)</td>
<td>1968, Pl. 1, figs. 1-4, 6, 7</td>
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<tr>
<td>Schrank (1969, Pl. 1, figs. 1-7, Pl. 2, figs. 1-5)</td>
<td>1983, Pl. 1, figs. 1-34</td>
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<tr>
<td>Odontopleura brevigna</td>
<td>Chatterton and Perry, 1983</td>
</tr>
<tr>
<td>Odontopleura (Odontopleura) arctica n. sp.</td>
<td>Figure 7.1-7.6</td>
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<tr>
<td>Diacanthaspis serotina</td>
<td>Apollonov, 1980</td>
</tr>
<tr>
<td>Apollonov (1980, Pl. 30, figs. 1-5)</td>
<td>1983, Pl. 2, figs. 1-20, Pl. 3, figs. 28-43</td>
</tr>
<tr>
<td>Odontopleura maccallai</td>
<td>Chatterton and Perry, 1983</td>
</tr>
<tr>
<td>Odontopleura (Odontopleura) nehedensis</td>
<td>Chatterton and Perry, 1983, Pl. 3, figs. 1-27</td>
</tr>
</tbody>
</table>

(Sinespinaspis) bombini is placed in tentative synonymy with O. (S.) nehedensis below, the taxa are treated separately for purposes of analysis. Some of the characters and character-states are illustrated and contrasted in Figures 2-4. The data were run on Swofford's (1985) PAUP program, treating all multistate (i.e., nonbinary) characters as unordered. Midpoint rooting was used, an option that roots the calculated Wagner Network at the midpoint of its longest branch, thereby determining the candidate trees for the choice of preferred cladogram.

Results. —Analysis yielded seven equally parsimonious Wagner Networks, each with a consistency index of 67.4 percent. This statistic was developed by Kluge and Farris (1969) and is a measure of the range of the data (the sum of the minimum number of character transformations implied by the data) divided by the length of the Network (the number of transformations required for the maximally parsimonious topology). When the seven candidate cladograms were congruency scored, two were found to be highest scoring, each accommodating 15 of the CIC's. These alternatives are shown in Figure 5. Note that they differ only in the relative positions of O. (Odontopleura) ovata and O. (Odontopleura) brevigna. The possible character-state assignments for the nonterminal nodes of each of the alternative cladograms are given in Tables 4 and 5. The consensus cladogram derived from the two maximally congruent rootings is shown in Figure 6, and should be taken as the most favored hypothesis of relationship as determined by the parameters of this study.

Discussion. —The analysis reveals two major species groups, each characterized by a suite of diagnostic features, and separated in the analysis by a branch length of 10. Each would appear to represent a natural phylectic group, and a distinction is thus made at the subgeneric level between the nominate subgenus and Taemasaspis n. subgen. A major question, which this analysis has not attempted to resolve, is whether or not the subgenera do in fact constitute sister taxa. If the subfamily is monophyletic, they do. In order to test this, it would be necessary to include in the analysis various species from what are assumed to be closely related genera.

SYSTEMATIC PALEONTOLOGY

Terminology. —One new term is introduced. Whittington (1956) and subsequent authors have used the term O₂ to refer to a spine pair on the occipital ring. Whittington's example (1956, fig. 1) was a Degree zero meraspid craniid of Apinanurus barbatis. Whittington. The intention, presumably, was that the holaspid occipital spine pair that develops from this juvenile pair should be called O₂. However, a distinction is required in many odontopleurine genera, including Odontopleura and Diacanthaspis, between the large abaxial occipital spines and a pair of smaller adaxially placed occipital spines. This latter pair would appear to represent the serial homologues of the major spine pairs found on the thoracic axes, at least in Odontopleura (Odontopleura) arctica (see Figure 7.1, 7.2, 7.4). Hence, this pair likely developed from the pair present in early ontogeny on the occipital ring, and strictly speaking should be called O₂. However, we do not wish to create confusion by altering the traditional description function of the term O₂ by insisting on a strict interpretation of homology, since in some cases whether or not the prominent occipital spines are serial homologues of the thoracic axial pairs is not immediately obvious. Therefore, whenever there occurs a prominent occipital spine pair, we suggest it should be referred to as O₂. Whenever it encloses a less prominent pair as in Odontopleura (Odontopleura), or whenever a nonprominent pair occurs in isolation as in some species of O. (Sinespinaspis), the less prominent pair should be referred to as O₂, designating paired axial-occipital spines (see Figure 2).

The following terms are used to distinguish between pygidial border spines. The "major border spines" are those that run from the pleural ribs derived from the first axial ring, regardless of their length. The "exterior pygidial border spines" are those that occur laterally to the major border spines. The "interior pygidial border spines" are those that occur between the major border spines.

TABLE 3—Character matrix for congruency analysis of Odontopleura. ? = missing data.

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Family ODONTOPLEURIDAE Bummeister, 1843
Subfamily ODONTOPLEURINAE Bummeister, 1843
Genus ODONTOPLEURA Emmrich, 1839

Type species.—Odontopleura ovata (Emmrich, 1839, p. 53; from a Graptolithengestein glacial erratic of late Wenlock to early Ludlow age, Nieder Kunzendorf, Silesia. By monotypy.

Diagnosis.—Odontopleurine trilobites with large 1L and 2L lobes; eyes small, nonpedunculate, set opposite middle or rear of 1L lobe, usually separated from glabella by at least width of 1L; 3L lobe rudimentary to absent; occipital lobes moderately developed to absent; large paired occipital spines may be present; numerous cephalic border spines (at least 15 on each free cheek), increasing in length posteriorly, at least posteriormost border spine occurring on lateral aspect of genal spine; genal spine slender, curved, length measured as straight line from tip to base slightly shorter to longer than length of free cheek measured as straight line from base of genal spine to anterior end of facial suture; thoracic segments with long to short tubular anterior spines and long, slender posterior spines; usually three dominant spine pairs on thoracic pleurae and a single dominant pair on rachis; second ring furrow of pygidium usually absent; 2–4 (rarely more) subequal interior pygidal border spines; 3–5 (rarely 2) pairs of exterior pygidal border spines; major pygidal border spines long and slender.

Discussion.—Whittington (1956) compared Odontopleura to Leonaspis, and later (1959, p. O504) provided a diagnosis for Odontopleura. Chatterton and Perry (1983) emended this diagnosis to accommodate the Llandovery species they assigned to the genus. Their diagnosis is itself emended above to reflect the concept of Odontopleura adopted in this paper.

Prantl and Přibyl (1949), in a major revision of odontopleurid trilobites, recognized only two species of Odontopleura, O. ovata Emmrich, 1839, from the Bohemian and Baltic Wenlock and Ludlow, and O. dufrenoiyi Barrande, 1846, from the Bohemian Wenlock. Snajdr (1979) rehabilitated O. prevosti Barrande, 1846, in a short note that referred to a single pathological specimen. Odontopleura prevosti had previously been considered a synonym of O. ovata by Prantl and Přibyl (1949) and Bruton (1968). Chatterton and Perry (1983) described a new Wenlock species from the Canadian Northwest Territories, O. brevigena, together with four Llandovery species that they considered best fit in an expanded concept of Odontopleura. These workers also proposed that Taemasaspis llandoveriana Snajdr, 1975, from the late Llandovery of Bohemia, be assigned to Odontopleura. Snajdr

![Figure 2](image1)
![Figure 3](image2)
believe, in agreement with Siveter (1989), that most of the names proposed or rehabilitated by Snajdr (1984b) should be considered synonyms of \emph{O. ovata}. Almost all are based upon little more than subjective assessments of spinosity, often between specimens from the same or equivalent horizons. We further question the validity of the lower Ludlow \emph{O. palava} Snajdr, 1984b. Siveter (1989, p. 142) accepted this species because of "the general lack of glabellar granules except for the larger paired granules . . . ." However, Snajdr (1984b) erected this taxon on the basis of five incomplete cranidia, and of the two figured, this lack of glabellar ornament is only distinct on the holotype (Snajdr 1984b, Pl. 1, fig. 8). The major paired spines dominate, but other spines and tubercles are clearly present, and the specimen shows some evidence of abrasion. The other figured specimen seems to have plenty of accessory granules on its glabella. With nothing known of the rest of the trilobite, these late representatives of the genus are not demonstrably distinct from \emph{O. ovata}, and should probably be referred to that taxon. In any case, the very brief descriptions and paucity of illustrations of taxa given by Snajdr (1984a, 1984b) make his proposals difficult to incorporate into detailed comparative studies.

**Subgenus Ivanopleura Snajdr, 1984**

\textit{Type species.} — \emph{Odontopleura dufrenoi} Barrande, 1846, from the Liten Formation (upper Wenlock, Monograptus flexilis to \textit{M. testis} zones), Svatý Jan pod Skalou, Loděnice, and Sedlec, Czechoslovakia.

\textbf{Odontopleura (Ivanopleura) dufrenoi} Barrande, 1846

\emph{Odontopleura dufrenoi} **BARRANDE**, 1846, p. 56.

\emph{Odontopleura dufrenoi} **Barrande**. \emph{Barrande}, 1968, p. 9, Pl. 1, figs. 5, 10 (with synonymy).

\emph{Miraspis rarrissima} \textit{Snajdr.} \textit{Snajdr}, 1975, p. 315, Pl. 2, fig. 4; \textit{Snajdr}, 1978, p. 32, Pl. 10, figs. 4-8, Pl. 12, fig. 10; \textit{Přibyl, Vaněk, and Hörniger}, 1986, p. 287.

\emph{Leonaspis pokornyi} \textit{Snajdr.} \textit{Snajdr}, 1975, p. 315, Pl. 2, fig. 8; \textit{Snajdr}, 1978, p. 35, Pl. 9, Figs. 15-18.

\emph{Ivanopleura dufrenoi} **(Barrande)**. \textit{Snajdr}, 1984a, p. 50, Pl. 1, Figs. 1-4 (with synonymy).

\emph{Ivanopleura rarrissima} **(Snajdr)**. \textit{Snajdr}, 1984a, p. 50, Pl. 1, figs. 5, 6, Pl. 2, figs. 1, 2.
**Discussion.** Śnajdr (1984a) erected *Ivanopleura* to accommodate *Odontopleura dufrenoi* Barrande and *Miraspis rarissima* Śnajdr. Siveter (1989, p. 137) expressed the opinion that in overall morphology these species so resembled *Odontopleura* that *Ivanopleura* was best considered a subgenus of that genus. We are of the opinion that similarities between the taxa have long been overestimated. With no new information to add, however, we follow Siveter (1989) and place *Ivanopleura* within *Odontopleura* (but see section on paleoecology and paleogeography below). As is evident from the above synonymy, there appear to be no objective differences between *O. (I.) dufrenoi* and the marginally older (latest Llandovery versus earliest Wenlock) *Miraspis rarissima* Śnajdr. Śnajdr (1984a) separated the species only by relative spinosities of the cephalon and dimensions of the pygidium. *Miraspis rarissima* is regarded here as a subjective junior synonym of *O. (I.) dufrenoi*.

Despite the lengthy taxonomic history of this species, it remains unsatisfactorily known. The specimens referred to it are generally incomplete cranidia and pygidia or severely abraded articulated individuals. That at least most of the cranidia belong together and represent a single distinct species seems certain. The following characters serve to distinguish *O. (I.) dufrenoi* from other species included in *Odontopleura*. The fixed cheeks are very narrow, and the eye is positioned less than the length of the 1L glabellar lobe from the glabella. The cephalic ornament consists of large, sparsely distributed tubercles, with the paired glabellar spines identifiable and occasionally prominent, whereas in mature holaspids of other *Odontopleura* species, the paired glabellar spines are indistinguishable from accessory glabellar spines and tubercles. There are strongly divergent O· spines. The O· spines occur laterally to the median occipital spine, on the axes of the O· spines. This contrasts with the condition in *O. (Odontopleura)*, where the O· spines are invariably placed posteriorly to the median occipital spine, and between the O· spines.

**Subgenus ODONTOPLEURA Emmrich, 1839**

**Type species.** — *Odontopleura ovata* Emmrich, 1839, from the upper Llandovery to lower Ludlow of Europe; *O. brevigena*...
Chatterton and Perry, 1983, from the Wenlock of the Mackenzie Mountains, Northwest Territories, Canada; O. (O.) arctica n. sp., from the lowermost Llandovery of the Canadian Arctic Archipelago; Diancathaspis serotina Apollonov, 1980, from the lowermost Llandovery of Kazakhstan.

Diagnosis.—Species of Odontopleura with O subgenus and anteriorly positioned median opisthalspine; 3S glabellar furrow visible at least ventrally; median ocipital spine placed distinctly forward from posterior border of cranidium, separated from posterior border by distance greater than one width of median ocipital spine; posteroventral (doubtful) part of posterior facial suture not directly opposite posterodorsal part; sutural ridge along posterior frontal suture on free cheek faint to absent; cephalic border spines on free cheek reduced to small denticles posterior to contact with anterior facial suture; anterior pleural spines elongate and tapering, especially on posterior thoracic segments; pygidium distinctly rounded and subsemicircular in ventral outline.

Discussion.—Members of this subgenus can be readily distinguished from those of Sinespinopsis n. subgen. by their possession of O, sinespinata, anteriorly positioned median ocipital spine, nonaligned posterior facial suture, denticulate as compared with fully developed anterior free cheek border spines, faint to absent as opposed to strongly developed sutural ridge along posterior frontal suture on free cheek, long as opposed to short and bar-like anterior pleural spines, and subsemicircular as opposed to subtriangular pygidium (see Figures 2–4).

Diancathaspis laokwunsangwanensis Lu and Chang, 1974, from uppermost Ashgill strata of Sichuan Province, China, may well belong to this subgenus. If so, it would represent the earliest known Odontopleura, and the only known Ordovician species. A thorough reinvestigation and additional material would be required to arrive at any firm taxonomic conclusions, however, and no attempt has been made to include the species in the present analysis.

Table 5—Possible character-state assignments for the nonterminal nodes of the cladogram of Figure 5.2. Format as in Table 4.

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**ODONTOPLEURA (ODONTOPLEURA) OVATA**
Emmrich, 1839

*Odontopleura ovata* Emmrich, 1839, p. 53, Pl. 1, fig. 3.

*Odontopleura (Odontopleura) ovata* Emmrich. Siveter, 1989, p. 138, Pl. 20, figs. 1–7, 11–21, Pl. 21, figs. 1, 3, 4, 8 (with full synonymy).

**Occurrence.**—Upper Llandovery to lower Ludlow of Bohemia (Bruton, 1968; Snajdr, 1984b); Wenlock to Ludlow of the Baltic Region (Bruton, 1967; Schrank, 1969; Alberti, 1970), Poland (Tomczykowa, 1957), Great Britain (Thomas, 1981); possibly the Silurian of the Carpathian Alps (Gartner, 1930); possibly the upper Wenlock of the Southern Ural (Bruton, 1968, p. 9); mid-upper Wenlock to lowermost Ludlow of the Annascul Inlier, County Kerry, Ireland (Siveter, 1989); non Wenlock to lower Ludlow of the Mackenzie Mountains, Northwest Territories, Canada (Chatterton and Perry, 1983, p. 18; Siveter, 1989, p. 142).

**Discussion.**—The taxonomic history of this species was discussed under the genus *Odontopleura*. Siveter (1989) has provided a comprehensive review.

*Odontopleura (O.) ovata* can be distinguished from the other three species included in the subgenus by the presence of dorsally expressed 3L glabellar lobes, relatively strongly developed ocipital lobes, eyes placed a transverse distance from the 1L lobe about subequal to the width of the 1L lobe as opposed to a distance greater than the width, and the presence of a weakly impressed second ring furrow on the pygidium (see Siveter, 1989, Pl. 20, figs. 12, 16, Pl. 21, fig. 4).

Chatterton and Perry (1983, p. 18) reported the possible occurrence of this species from upper Wenlock to lower Ludlow strata of the Dolorrme Range of the Mackenzie Mountains. The available material is still insufficient to allow proper specific assignment. However, it does not represent a Laurentian occurrence of *O. (O.) ovata*, as it clearly lacks the distinctive glabellar morphology (well-defined 3L and ocipital lobes) of that...
species. The material may represent a distinct new species, or possibly a variant of O. (O.) brevigena, with longer O₃ spines. Proper description will await the accumulation of adequate material.

**ODONTOPLEURA (ODONTOPLEURA) BREVIGENA**  
Chatterton and Perry, 1983

*Odontopleura brevigena* CHATTERTON AND PERRY, 1983, p. 18, Pl. 1, figs. 1–34.

*Odontopleura perpeta* ŚNAJD, 1984b, p. 103, Pl. 2, figs. 1, 2.

*Odontopleura (Odontopleura) brevigena* Chatterton and Perry, SIVETER, 1989, p. 142.

**Occurrence.** Wenlock of the Mackenzie Mountains, Northwest Territories, Canada.

**Discussion.** It should be noted that Chatterton and Perry's (1983, Pl. 1, figs. 6–9) holotype has a teratological pygidium, with five interior pygidial border spines. Further specimens collected from the type locality have yielded two more teratological pygidia, each with six fully developed interior pygidial border spines. Such examples are rare, however, as these specimens compare with dozens of normal pygidia collected from the same locality.

*Odontopleura (O.) brevigena* differs from the other species assigned to the subgenus in the presence of a hypostome with a distinctly crenate posterior margin (see Chatterton and Perry, 1983, Pl. 1, figs. 16, 25), relatively short O₂ spines, and having genal spines distinctly shorter than the remainder of the free cheek.

As noted by Siveter (1989, p. 142), *O. perpeta* Śnajd, 1984b, seems very similar to *O. (O.) brevigena*, and may be a junior synonym. The Bohemian material, however, is as yet too poorly known to permit a proper comparison.

**ODONTOPLEURA (ODONTOPLEURA) SEROTINA**  
(Apollonov, 1980)


**Occurrence.** Lowesterr M. Kazakhstan.

**Discussion.** Although not especially well known, the form of the cranium and free cheek leaves no doubt that this species belongs in the subgenus. It appears to be closely related to the contemporaneous *Odontopleura (Odontopleura) arctica* n. sp., united in particular by the distinctive anterior facial sutures, which are initially divergent and do not begin to converge until opposite the middle of the 2L glabellar lobe. The pygidium, if correctly associated, is unusual for *Odontopleura*, as the major border spines do not appear to be exceedingly long and the dorsal surface is much less spinose than normal.

*Odontopleura (Odontopleura) serotina* can be distinguished from all other species assigned to the subgenus particularly by its deep axial furrows, which separate the anterolateral portion of the 1L glabellar lobes from the fixed cheeks, and by the presence of much shorter major pygidial border spines. *Odontopleura (O.) serotina* and *O. (O.) arctica* n. sp. differ collectively from the other two species assigned to the subgenus by the presence of initially divergent anterior facial sutures and the presence of three, as opposed to four, external pygidial border spines. *Odontopleura (O.) serotina* differs further from *O. (O.) arctica* n. sp. in having a much narrower, slightly longer, and much less spinose pygidium.

It is acknowledged that some of these differences could be due to the quality and mode of preservation. That *O. (O.) serotina* represents a distinct species, phylogenetically close to *O. (O.) arctica*, does not seem at issue. More and better illustrated material would be required, however, for a truly satisfactory differential diagnosis.

**ODONTOPLEURA (ODONTOPLEURA) ARCTICA** n. sp.

*Figure 7.1–7.6*

**Material.** Holotype GSC 95875, an external mold of a complete individual. Paratypes GSC 95876, an external mold of a complete individual; GSC 95877, an internal mold of a complete individual; GSC 95878, an associated cranium, two free cheeks, and thoracic segment; GSC 95879, a pygidium with original shell material preserved; GSC 95880, an isolated thoracic segment (not figured). All from a single block of shale, a glacial erratic collected from the Marshall Peninsula, northwest coast of Cornwallis Island, Canadian Arctic, and assigned to the lowermost Llandovery, Cape Phillips Formation.

**Diagnosis.** A species of *Odontopleura (Odontopleura)* with 3L glabellar lobes defined ventrally only; axial furrows very shallow at anterior of 1L glabellar lobes; occipital spines weakly defined; eyes placed a transverse distance from 1L glabellar lobe greater than width of 1L lobe; O₂ spines long, reaching as far as 6th thoracic segment; anterior facial sutures long and divergent opposite 2L glabellar lobe; posterolateralmost cranial marginal spine long, extending to middle of 2nd thoracic segment; genal spine subequal in length to slightly longer than remainder of free cheek; pygidium with three pairs of exterior border spines; major pygidial border spines of at least three times as long as exagittal length of pygidium measured directly anterior to them; pygidium approximately four times as wide as sagittal length; second ring furrow of pygidium wholly absent.

**Discussion.** A comparison with *Odontopleura (Odontopleura)* serotina may be found under the discussion of that species.

*Odontopleura (Odontopleura) arctica* differs from *O. (O.) brevigena* in having longer O₂ spines; anterior facial sutures that are divergent, as opposed to convergent opposite the 2L glabellar lobes; longer posterolateralmost cranial marginal spines; longer genal spines; three as opposed to four exterior pygidial border spines; and longer major pygidial border spines.

*Odontopleura (Odontopleura) arctica* differs from *O. (O.) ovaia* in lacking dorsally expressed 3L glabellar lobes; having weak as opposed to strongly defined occipital lobes; eyes placed a greater transverse distance from the 1L glabellar lobes; anterior facial sutures divergent as opposed to convergent opposite 2L glabellar lobes; longer posterolateralmost cranial marginal spines; three as opposed to four pairs of exterior pygidial border spines; longer major pygidial border spines; pygidium about four, as opposed to three, times as wide as sagittally long; lacking any impression of the 2nd ring furrow of the pygidium. GSC 95878 (Figure 7.5) appears to represent a molt ensemble. The configuration of the associated elements indicate that this species behaved during ecdysis in a manner similar to that of *O. (O.) brevigena* (Chatterton and Perry, 1983, p. 19, Pl. 1, figs. 1–4), the only other species of *Odontopleura* for which evidence for such behavior has been presented. Molting in both of these species involved a separation and rotation of the free cheeks and displacement of the hypostome. According to Chatterton and Perry (1983, p. 19), the trilobite then crawled out from beneath the remaining articulated elements and over the separated hypostome and free cheeks. This analysis is supported here, as the cranium (Figure 7.5) has clearly remained in close articulation with the 1st thoracic segment.

**Subgenus SINESPINASPIS** n. subgen.

**Type species.** *Odontopleura greenwoodii* Chatterton and Perry, 1983.

**Etymology.** From the Latin preposition sine, without, the Latin noun spina, spine, and the Greek noun aspis, a shield. Gender is feminine.

**Species included.** *Odontopleura greenwoodii* Chatterton and Perry, 1983; *Odontopleura maccalii* Chatterton and Perry, 1983;
Odontopleura nehedensis Chatterton and Perry, 1983; Odontopleura bombini Chatterton and Perry, 1983; all from the Llandovery of the Mackenzie Mountains, Northwest Territories, Canada; Taemasaspis llanowegozya Snajdr, 1975, from the Llandovery of Bohemia.

Diagnosis.—Odontopleurine trilobites with 3L glabellar lobes usually completely absent; occipital lobes usually weak or absent; occipital furrow usually shallow and indistinct; occipital ring with O₃, spines only, or entirely lacking paired occipital spines; O₂, never developed; anterior facial sutures generally short, subparallel to convergent opposite 2L glabellar lobe; spine usually absent from posterolateralmost aspect of cranidial margin; median occipital spine either at posterior cranial margin or within one median spine width from margin; genal spine usually shorter than remainder of free cheek; posteroventral (doubtful) part of posterior facial suture aligned with posteroventral part; strong sutural ridge along posterior facial suture on free cheek; cephalic border spines at anterior of free cheek persist as fully developed spines to contact with anterior facial suture; anterior pleural spines very short and barb-like; number of interior pygidial border spines may be reduced in number to two; pygidium subtriangular in ventral outline, usually with an anterior inflection of the median ventral doublure.

Discussion.—This subgenus was contrasted with Odontopleura (Odontopleura) under the discussion of that subgenus.

ODONTOPLEURA (SINESPINASPIS) GREENWOODI

Chatterton and Perry, 1983

Odontopleura greenwoodi CHATTERTON AND PERRY, 1983, p. 19, Pl. 2, figs. 1–20, Pl. 3, figs. 28–43.

Occurrence.—Middle Llandovery (Pteraspithodus celloni zone) of the Mackenzie Mountains, Northwest Territories, Canada.

Discussion.—An autapomorphy of Odontopleura (Sinespinaspis) greenwoodi among all species of Odontopleura is the presence of two, as opposed to one, free cheek border spines occurring on the lateral aspect of the genal spine.

Because Odontopleura (Sinespinaspis) greenwoodi is both the best known and stratigraphically longest ranging species assigned to the subgenus, it was chosen as the type species. It has, however, many morphological features that would tend to ally it with those species included in O. (Odontopleura), including long and convergent anterior facial sutures, small spines present on the posterolateral cranidial margins, and long genal spines. It does, however, have in common with the other species assigned to O. (Sinespinaspis) a suite of uniquely shared characters, just as O. (Odontopleura) is defined by a similar suite (as shown by the cladograms of Figure 5).

An argument could be put forward for the presence of O₃ spines in Odontopleura (Sinespinaspis) greenwoodi. The occipital ring (Chatterton and Perry, 1983, Pl. 2, figs. 1, 7, Pl. 3, figs. 29, 30, 32) typically has two pairs of occipital spines. The median pair corresponds to the dominant pairs on the thoracic axes and represents O₃. The lateral pair could therefore be construed as O₂ and be taken as homologues of the large O₃ spines of O. (Odontopleura). The O₂ spines of that subgenus, however, have no obvious serial homologues on the thoracic axes. The lateral spine pair of O. (S.) greenwoodi has very clear serial homologues (contrast Chatterton and Perry, 1983, Pl. 2, figs. 1, 3). Hence, while topologically similar structures, the evidence suggests that the lateral spine pair of O. (S.) greenwoodi and the O₃ spines of members of O. (Odontopleura) are non-homologous.

ODONTOPLEURA (SINESPINASPIS) MACCALLAI

Chatterton and Perry, 1983


Occurrence.—Llandovery (Pteraspithodus celloni zone) of the Mackenzie Mountains, Northwest Territories, Canada.

Discussion.—Odontopleura (Sinespinaspis) maccallai can be distinguished from O. (S.) greenwoodi by the presence of shallower longitudinal furrows at the posterior of the IL glabellar lobes, a slightly deeper and better defined occipital furrow, the absence of O₃, spines, short and subparallel anterior facial sutures, lack of posterolateral cranidial marginal spines, a much shorter genal spine, and a variable (2–4) number of interior pygidial border spines, as opposed to a constant four.

Odontopleura (Sinespinaspis) maccallai differs from O. (S.) nehedensis in the following features: axial furrows at anterior of IL glabellar lobes shallow as opposed to deep; occipital lobes weakly defined as opposed to wholly absent; occipital furrow shallow but evident as opposed to indistinct; eyes placed transversely farther from the IL glabellar lobes; O₃ spines absent; and four as opposed to three pairs of exterior pygidial border spines.

ODONTOPLEURA (SINESPINASPIS) LLANDOVERYANA

(Snajdr, 1975)

Taemasaspis llanowegozya Snajdr, 1975, p. 314, Pl. 1, fig. 6, Pl. 2, fig. 7; Snajdr, 1978, p. 28, Pl. 7, figs. 1–12, Pl. 8, figs. 9–14, Pl. 12, fig. 3; Ramsköld, 1984, p. 249; Přibyl, Vaněk, and Höhninger, 1986, p. 267.


Taemasaspis llanowozyana Snajdr. SIVETER, 1989, p. 137.

Occurrence.—Upper Llandovery, Hýskov area, near Beroun, Czechoslovakia.

Discussion.—The association of the sclerites figured by Snajdr (1975, 1978) as Taemasaspis llanowozyana has been questioned by Přibyl et al. (1986), who considered most of the material to belong to Primaspis (Meadowtownella), with some of the pygidia (they did not specify which) referred to Miraspis rarissima Snajdr, 1975, a species they included in Odontopleura. Following Chatterton and Perry (1983) and Siveter (1989), the figured cranidia seem more similar to the Mackenzie Mountains Llandovery species here grouped in Odontopleura (Sinespinaspis) than to Primaspis (Meadowtownella). That most of the pygidia figured by Snajdr (1978) belong with the cranidia seems reasonable, since his Plate 7, figure 7 illustrates the dorsal surface of a relatively well-preserved articulated exoskeleton, confirming the association. Snajdr's (1978) Plate 8, figure 12 would appear to be the only questionable assignment, and was not used in the cladistic analysis herein (see Table 2).

The relationships of this species are somewhat problematic. By parsimony, there are two equal length networks differing in their placement of Odontopleura (Sinespinaspis) llanowozyana (one of which was discarded by congruency). This is partly a problem of the material available and the standards of preservation and illustration of that material. Of more consequence, however, is the simple fact that, with regard to the subgenus, O. (S.) llanowozyana is highly autapomorphic. It has no fewer than five character-states (in characters 1, 4, 5, 20, and 21) not shared with any other member of the subgenus. Following this, O. (S.) llanowozyana may be distinguished from all other species included in Sinespinaspis by the following features: 3L glabellar lobes expressed dorsally; occipital lobes strongly defined; occipital furrow deep; pygidium about four, as opposed to three, times as wide as long; and strongly impressed 2nd ring furrow of pygidium present.

An undescribed odontopleurine species from the Llandovery of the Forbes district, New South Wales, closely resembles Odontopleura (Sinespinaspis) llanowozyana (L. Sherwin, personal commun.). This material consists of well-preserved ex-
ternal molds of articulated individuals, and its description should provide a sound basis for comparison and evaluation of the Bohemian material.

**Odontopleura (Sinespinaspis) nehedensis**
Chatterton and Perry, 1983


*Odontopleura bombini* CHATTERTON AND PERRY, 1983, p. 22, Pl. 4, figs. 1–16.

Occurrence.—Middle to upper Llandovery (Pierospadodus celloni to *P. amorphognathoides* zones) of the Mackenzie Mountains, Northwest Territories, Canada.

Discussion.—Chatterton and Perry (1983) recognized *Odontopleura* (*Sinespinaspis*) nehedensis and *O. (S.) bombini* as separate species. They speculated (p. 13) that the slightly older *O. (S.) nehedensis* might be a direct ancestor of *O. (S.) bombini*, the latter occurring 37 m higher in the same section (each occurs by itself in other sections, but only in section AV 1 are they found in stratigraphic succession). They did not provide a differential diagnosis for the species. From a purely morphological standpoint, the species differ only in the relative depth of the longitudinal furrows at the posterior of the 1L glabellar lobes, the position of the median occipital spine, and the number of interior pygidial border spines. Of these, the first could be a function of preservation and of comparison of differently sized specimens, as all available *O. (S.) bombini* material is very small (Chatterton and Perry, 1983, p. 23). The second seems genuine, with the median spine set very slightly forward from the posterior craniol margin in *O. (S.) nehedensis* but directly at the margin in *O. (S.) bombini*. As for the condition of the pygidial border spines, the number of interior spines ranges from 2 to 4 in *O. (S.) nehedensis*, but is restricted to two in *O. (S.) bombini*. The entire sample of pygidia of *O. (S.) bombini* is quite small, however, and this character exhibits some variability even in species for which the number is all but constant (see *O. (O.) brevigenera* above). In all other aspects of morphology, *O. (S.) nehedensis* and *O. (S.) bombini* are identical, and given the discussion above, distinction between them is of very limited biostatigraphical utility. The possibility must therefore be acknowledged that the two taxonomic species represent temporarily separated populations of the same phyletic lineage. Therefore, pending further information, they are placed in questionable synonymy.

*Odontopleura* (*Sinespinaspis*) nehedensis was contrasted with *O. (S.) maccallai* under the discussion of that species. It may be distinguished from *O. (S.) llandoveriana* by the absence of the latter species' many autapomorphies. *Odontopleura* (*S.) nehedensis differs from *O. (S.) greenwoodi* in the following features: axial furrows at anterior of 1L glabellar lobes deep as opposed to shallow; occipital lobes entirely absent; eyes placed transversely nearer to the 1L glabellar lobes; anterior facial sutures shorter; no spines at posterolateral part of craniol margin; genal spines shorter than remainder of free cheeks; one as opposed to two border spines occurring on lateral aspect of genal spines; three as opposed to four pairs of exterior pygidial border spines; and usually less than four as opposed to four (or more) interior pygidial border spines.

**PALEOEKOLOGY AND PALEOGEOGRAPHY**

Studies of Silurian trilobite paleoecology are few, but include Thomas (1980), Mikulic (1980), Mikulic and Watkins (1981), Mannl (1982), and Chlupáč (1987). Both subgenera of *Odontopleura* were widely distributed. Hence, no particular paleobiogeographic pattern can be recognized among the 10 known species. This broad distribution seems likely to have been directly related to the trilobites' choice of habitat. All of the species included in *Odontopleura* had, on present evidence, a relatively narrow ecological valence, preferring the deeper waters of the outer shelf or of the shelf-slope transition zone. An exception is *Odontopleura* (*Ivanopleura*) *dufrenoi*. This Bohemian species occurs in shallow-water deposits, included by Chlupáč (1987) in his *Bumastus*–*Sphaerexochus*–*Chetrurus* assemblage, which assigned to Boucot's (1975) Benthic Assemblage 3 or 2. Thus, the doubt expressed above about the systematic position of this species is borne out by an ecological division between it and all other species included in *Odontopleura*.

*Odontopleura* (*Sinespinaspis*) *llandoveriana* is included by Chlupáč (1987) in his *Ivanopleura*–*Aulacopleura* assemblage, assigned to Boucot's (1975) Benthic Assemblage 4. *Odontopleura* (*Odontopleura*) *ovata* is included by Chlupáč (as *O. preovi*); in his *Aulacopleura konincki* assemblage, assigned to Boucot's (1975) Benthic Assemblage 4 or 5. The Irish *O. (O.) ovata* material was regarded by Siveter (1989, p. 156) as occurring in a distal shelf environment. All of the Mackenzie Mountains species are known from relatively deep water, distal shelf-slope environments (Chatterton and Perry, 1983). The drift block upon which the known specimens of *O. (O.) arctica* n. sp. occur is composed of dark, fine-grained, argillaceous, micritic limestone. The only other fossils present are the above-mentioned graptolite fragments and a single pedicle valve of a smooth arthropod, possibly athyridid, brachipod. The lithology of the sample, the presence of graptolites, and the undisturbed nature of the articulated trilobites suggest a low-energy, probably low-oxygen, deep-water environment. As deeper water forms, therefore, members of *Odontopleura* were not subject to the endemism of more onshore species, having wider opportunities for dispersal and being less affected by eustatic sea-level fluctuations. This accounts for their almost global distribution through Early and Middle Silurian times.

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**REFERENCES**


THE UPPER DEVONIAN (FRASNIAN) CONODONT SEQUENCE IN THE LIME CREEK FORMATION OF NORTH-CENTRAL IOWA AND COMPARISON WITH LIME CREEK AMMONOID, BRACHIOPOD, FORAMINIFER, AND GASTROPOD SEQUENCES

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ABSTRACT—The Upper Devonian (Frasnian) conodont fauna of the Lime Creek Formation of north-central Iowa is dominated by species of Polygnathus. Patterns of species composition and abundance are consistent with the Polygnathus biofacies described from the Frasnian of the Northwest Territories of western Canada. Consequently, the standard Frasnian conodont zones, defined on sequences developed in the Palmatolepis biofacies, are not applicable to the Lime Creek sequence. The Lime Creek conodont sequence correlates with Zones 4, 5 and Faunal Interval 7 of the Frasnian conodont sequence in the Alberta Rockies and with similar sequences in the southwestern United States. The Pb elements of Palmatolepis semichatovae Ovatannova and Ancyrognathus deformis (Anderson) are described and illustrated for the first time.

In the Lime Creek Formation of north-central Iowa, brachiopods of the lowermost part of the Nervostrophia thomasi Zone of Day (1989a) occur in Zone 4, brachiopods of most of the N. thomasi, Douvillina arcuata, and Cyrtospirifer whyneti Zones span conodont Zone 5, and the Elita inconsoneta and Iowatrypa owenensis Zones occur in Faunal Interval 7. Species of the ammonoid Manticoceras and of the gastropods Floyda, Turbonopsis, and Westenia are restricted to Faunal Interval 7. Species of the calcareous foraminifer Nancicella first occur in Zone 5, and are joined by species of Multisepitida high in Zone 5.

INTRODUCTION

This study outlines the Frasnian conodont sequence as it is developed in three sections of the Upper Devonian Lime Creek Formation in north-central Iowa (Figures 1–3). Detailed knowledge of the conodont sequence allows for calibration of Lime Creek brachiopod zones, as well as biostratigraphically useful calcareous foraminifers, ammonoids, and selected gastropods in the upper Frasnian of the Iowa Basin in the U.S. Midcontinent.

Strata of the Lime Creek Formation in north-central Iowa record open- and restricted-marine deposition in cratonic-shelf and shelf-margin settings (Figure 4). The Lime Creek conodont fauna differs significantly from those of the Palmatolepis biofacies developed in offshore equivalents in eastern Iowa (Sweetland Creek Shale) and the Selmier Shale in the Illinois Basin (Figure 4). Composition and patterns of species abundance of Lime Creek conodont faunas discussed here and by Metzger (1989) are similar to those described from the Frasnian Polygnathus biofacies by Klapper and Lane (1985).

Owing to the dominance of species of Polygnathus and general absence of Palmatolepis, Ancyrognathus, and Ancyrodeilea, direct correlations of the Lime Creek sequence with the standard conodont sequence developed in the Frasnian Palmatolepis biofacies (Ziegler, 1958, 1962) is not possible. However, the Lime Creek and related conodont sequences in the Frasnian of New Mexico and Arizona are correlated directly with Zones 4, 5, and Faunal Interval 7 of the Alberta Rockies zonation of Klapper and Lane (1989) in which the divisions above Zone 4 are defined by elements of the Polygnathus biofacies.

PREVIOUS INVESTIGATIONS

The first study of the Lime Creek conodont fauna was by Anderson (1964, 1966). Nearly all specimens identified as Palmatolepis gigas by Anderson (1966) are now placed in P. semichatovae (see synonymy of P. semichatovae in Klapper and Lane, 1985, and this study), which necessitates revision of Anderson's (1966) assignment of the Lime Creek to the Lower Palmatolepis gigas Zone (cited in Klapper et al., 1971, p. 302). Other important species illustrated by Anderson (1966) include Palmatolepis foliacea and Polygnathus deformis (here questionably assigned to Ancyrognathus, following the usage of Metzger, 1989).

Day (1987) established ranges of species of the gastropod genera Floyda and Turbonopsis relative to conodonts in the Lime Creek Formation. Day (1989a) discussed the distribution of conodont faunas with respect to the brachiopod zonation in the Lime Creek in northern Iowa (Figure 2).

Metzger (1989) described Polygnathus-dominated conodont faunas and calcareous foraminifers from shallow-water facies of the subsurface Lime Creek Formation in north-central Iowa and southeastern Nebraska, and proposed correlations similar to those presented in this study. However, because the Lime Creek conodont faunas reported by Metzger lack species of Palmatolepis, they cannot be correlated directly with the Alberta Rockies Frasnian zonation of Klapper and Lane (1989).

LITHOSTRATIGRAPHY AND DEPOSITIONAL AND PALEOGEOGRAPHIC SETTING

Witzke (1987) delimited major facies tracts and discussed the depositional setting of the Lime Creek Formation and its equiv-