

# Anisian (Middle Triassic) ammonoids from North America: quantitative biochronology and biodiversity

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**ABSTRACT:** This study synthesizes and revises the ammonoid zonation as well as their correlation with each other for western Nevada (USA), British Columbia (Canada), and the Sverdrup Basin (Canada) by utilizing the unitary association method. Based on a standardized taxonomy, the Anisian in the studied areas contains 13, 10, and 3 zones and a total of 174, 90, and 7 species, respectively. The zonation is correlated by means of a 'common taxa zonation', which includes all taxa common to the studied basins. This leads to new and more precise correlations, which are at slight variance with those of the literature. Hence, the *Buddhaites hagei* Zone (Canada) correlates only with the *Intornites mcTaggarti* Subzone (Nevada) and not with the entire *Acrochordiceras hyatti* Zone (Nevada). The *Tetsaoceras hayesi* Zone (Canada) appears to correlate with the *Unionvillites hadleyi* Subzone (Nevada) of the *hyatti* Zone and not with the *Nevadisculites taylori* Zone. The *Hollandites minor* Zone (Canada) more than likely correlates with the *taylori* Zone (Nevada) rather than the *Balatonites shoshonensis* Zone as is usually acknowledged. The unitary association method enables us to quantify the diachronism of the studied taxa, which affects about 67% of the genera and 18% of the species common to Nevada and British Columbia. Therefore, this diachronism is significant and its value for correlation should not be overlooked. Finally, a diversity analysis based on the revised zonation is performed. This analysis reveals that the major event occurred during the Nevada *hadleyi* Subzone (early Middle Anisian), which in Nevada and British Columbia, records the highest species richness of the Anisian as well as enhanced exchanges between usually latitudinally restricted faunas. This event may reflect significant changes in climate or oceanic circulation at that time.

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## INTRODUCTION

Triassic ammonoid zonation was European in nature (Tozer 1984), since most Triassic stages were first defined in the Alps. Hence, they have usually been considered as the standard, reference zonal sequences for the Triassic. However, most of these zonation schemes were flawed by a typological taxonomy, which resulted in far too many arbitrary species, as well as poor superpositional control, and the condensed occurrence of several faunas (Tozer 1971, 1994b; Brack and Rieber 1993; Balini, in Gaetani 1993). The Anisian stage (early Middle Triassic; 245–240.7 Ma, Gradstein and Ogg 2004; Mundil et al. 1996) serves as an illustrative example of these problems. Consequently, the European sequence of Anisian ammonoid zones still lacks consensus and even though a thorough taxonomic revision is needed, progress is being made towards resolving these conflicts (e.g. Brack and Rieber 1986, 1993, 1996; Balini 1992a, b, in Gaetani 1993; Gaetani 1993; Mietto and Manfrin 1995; Brack et al. 1995, 2003; Mietto et al. 2003; Vörös et al. 2003).

At present, the newer, more refined North American zonation is known to be more robust and is based on a coherent taxonomy (Tozer 1971, 1994b). Indeed, the biochronology of the North American Triassic is based on what is probably the world's most complete sequence of Anisian ammonoid faunas. The current debate on the definition of the Anisian/Ladinian boundary in Europe (e.g. Vörös 1993; Brack and Rieber 1994; Brack et al. 2003; Mietto et al. 2003; Vörös et al. 2003; and the final 2005 decision of the Subcommission on Triassic Stratigraphy) as well as the discovery of important new faunas in North America during the last few decades has prompted this revision. Indeed, some of these new faunas bring to the forefront major changes in the standard zonation and new correlations across the North

American plate-bound series (as opposed to accreted terranes), as well as with the European sequence.

## GEOLOGIC SETTING

Marine Triassic rocks yielding rich Anisian ammonoid faunas occur around the Pacific and Arctic oceans, as well as in the Tethyan belt, which comprises the Alps, Turkey, Iran, southern Tibet, southern China, and Indonesia (Tozer 1984). This study takes into account the following three basins distributed along a paleolatitude gradient in the Cordillera of western North America: Nevada, British Columbia, and the Sverdrup Basin. The relative positions of these three basins have remained unchanged since Triassic times, thus providing a paleogeographical latitudinal transect (text-fig. 1).

Triassic rocks of the Sverdrup Basin provide a record of marine facies from the Lower Griesbachian to the Upper Norian. Anisian faunas occur in the Schei Point and Blaa Mountain formations, which are composed of shales, siltstones and sandstones. Triassic rocks of British Columbia belong to the plate-bound series of the tectonic Eastern Belt (Rocky Mountains). Anisian faunas occur in the Toad Formation, which consists mainly of dark gray calcareous siltstone and shale. Most of the Triassic ammonoid faunas known from Canada occur in a similar biofacies in which the ammonoids are associated with other fossils indicative of a pelagic habitat (e.g. radiolarians, conodonts, thin-shelled bivalves such as *Daonella*). Tozer (1994a) provided a brief geologic review of these two Canadian areas.

Triassic rocks of northwestern Nevada belong to a shallow marine shelf terrane (Speed 1978), in which sedimentation rates were controlled by differential uplift and subsidence resulting from an incipient extension of northwestern Nevada following

the Sonoma orogeny (Wyld 2000). The studied areas are therefore parautochthonous with respect to the North American craton (Wyld 2000). A detailed stratigraphical analysis of the basin was worked out by Silberling and Wallace (1969) and Nichols and Silberling (1977) following many years of intensive work. Anisian faunas occur in the Fossil Hill Member, which is common to the Favret and Prida formations of the Star Peak Group. Lithologically, the Fossil Hill Member is mainly composed of thin-bedded, dark micritic limestones alternating with silty shales, which were deposited in an oxygen-poor basin. Ammonoids occur with radiolarians, conodonts, halobiid bivalves, other cephalopods, fishes, and ichthyosaurs.

## TAXONOMIC NOTES

The data utilized for the biochronological analysis have been compiled from multiple sources (new field data and literature) in which taxonomic definitions may be at variance. In order to establish reliable correlations and to avoid inconsistencies between the zonations for each basin, it becomes necessary to first achieve a standardized taxonomy. The use of each species name must be consistent throughout the entire data set. It must also account for intraspecific variability and for ontogenetic changes. Note that inherent limitations to this standardization are obviously imposed by the quality of available taxonomic data (i.e. plots of occurrences against lithologic columns and illustration of intraspecific variability and ontogeny). It is noteworthy that we used a population approach to identify species, since ammonoids may display a large intraspecific variability and covariation of characters (the 1<sup>st</sup> Buckman law of covariation), which ranges from compressed, involute, weakly ribbed forms to more depressed, more evolute, strongly ribbed forms (e.g. Reeside and Cobban 1960; Callomon 1985; Dagens and Weitschat 1993; Checa et al. 1997). For further details, see Tozer (1971) and Monnet and Bucher (in press).

The standard biochronological scheme for the Anisian was produced: 1) by Silberling and Wallace (1969), Silberling and Nichols (1982), and Bucher (1988, 1989, 1992a, b; 1994) for Nevada, 2) by Silberling and Tozer (1968), Tozer (1967, 1982, 1994a) and Bucher (2002) for British Columbia, and 3) by Tozer (1994a) for the Sverdrup Basin. These works, based on bed-by-bed sampling, revealed that the Nevada sequence should be considered as the world's most complete sequence for low paleolatitude Anisian ammonoid faunas. Therefore, the data necessary for the correlation of North American Anisian ammonoid biochronology were derived from the references cited above. Bucher and Orchard (1995) also provided additional preliminary taxonomic and biochronological data for ammonoids spanning the Anisian/Ladinian boundary.

This study also includes recent, unpublished data from British Columbia (occurrence of the *Parafrechites meeki* Zone near the Alaska Highway) and northwestern Nevada (occurrence of the *Paracrochordiceras americanum* Zone in the northern New Pass Range), which add significantly to the correlations. Recent investigations in the Augusta Mountains (northwest Nevada) bring to the forefront additional new faunas whose taxonomy have been analyzed and described by Monnet and Bucher (in press) in a thorough monographic treatment. These new faunas enable the recognition of: 1) two new zones at the base of the Late Anisian, namely the *Gymnotoceras weitschati* and *G. mimetus* zones, bracketed between the *Balatonites shoshonensis* and *Gymnotoceras rotelliformis* zones, 2) a new subzone in the latest Middle Anisian (*Bulogites mojsvari* Subzone), and 3) a revision of the subdivisions of the

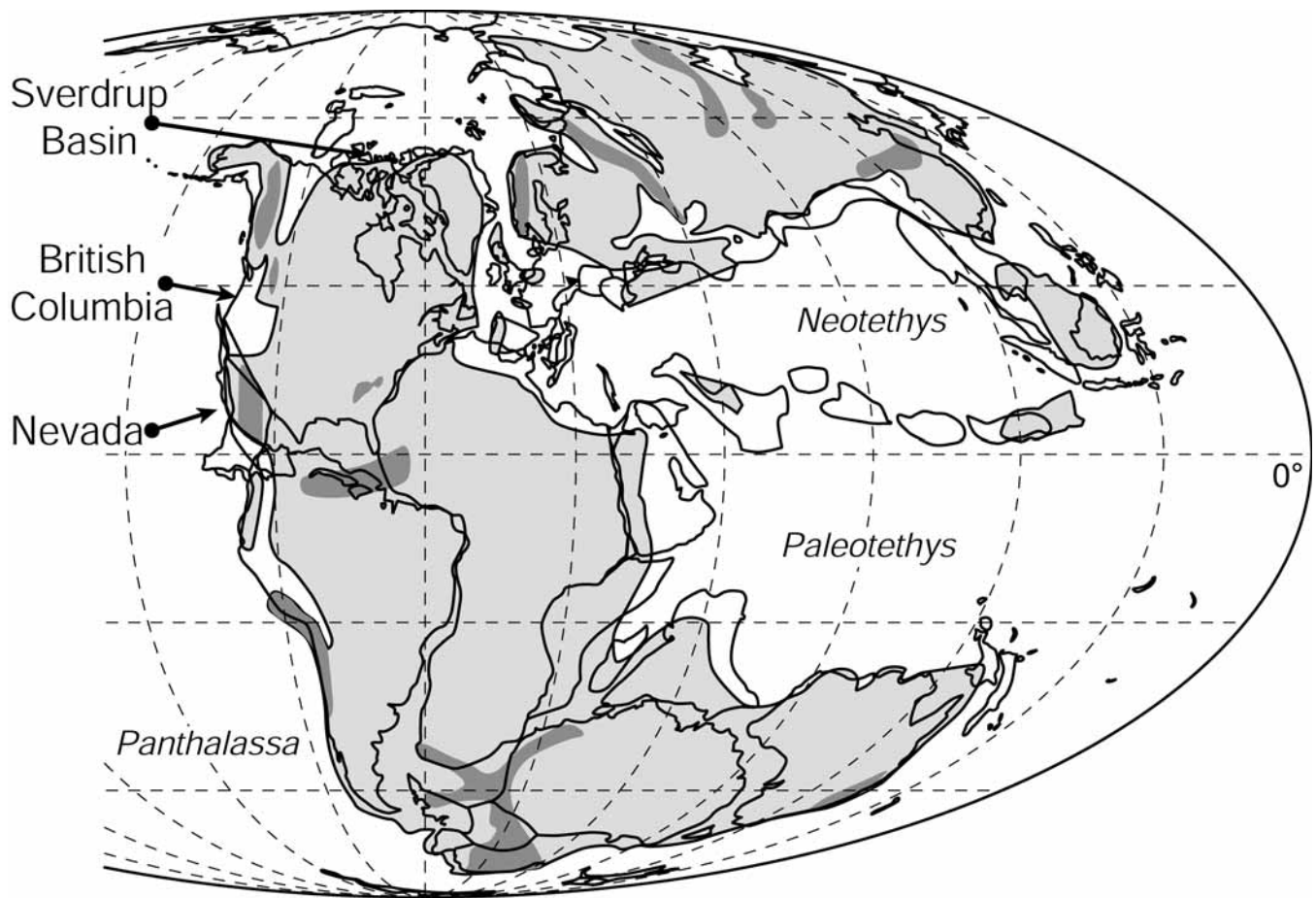
*rotelliformis* Zone (text-fig. 2). These new faunas also lead to the recognition of 11 new genera and 15 new species, as well as the revision of several species defined by Smith (1914), but subsequently considered as junior synonyms by Spath (1934) and Silberling and Nichols (1982). Text-figure 3 displays the synthetic biochronological distribution of these faunas. In addition to their taxonomic and biochronological importance for correlation with the European sequence, these faunas are also of essential significance for the phylogenetic reconstruction of the Paraceratitinae.

## BIOCHRONOLOGY

### Zonation method

The chronological component of the ammonoid fossil record is assessed here by utilizing the unitary association method (UAM). This method, created by Guex (1977, 1991), is favored since it is acknowledged to have the following invaluable advantages: 1) it is a quantitative and deterministic method based on the coexistence of species; 2) it constructs discrete (non-continuous) biozones in agreement with the discontinuous nature of the fossil record; 3) it preserves the integrity of the original data set (i.e. all raw documented associations of taxa – coexistence in space – are preserved and no reversed sequences of ranges are created), contrary to most other biochronological methods (e.g. probabilistic and multivariate treatments of local first and last appearance datums; see discussion in Baumgartner 1984a and Boulard 1993); 4) its efficiency in solving complicated biochronological problems has been demonstrated with taxonomic groups having a much less favorable record than ammonoids (e.g. radiolarians: Baumgartner 1984b; Baumgartner et al. 1995; O'Dogherty 1994; Carter et al. 1998; micromammals: Guex and Martinez 1996; dinoflagellates: Edwards and Guex 1996; nannoplankton: Boulard 1993); 5) it usually involves a two or threefold increase in biochronological resolution, even in the case of ammonoids (for examples, see Monnet and Bucher 1999, 2002), which are traditionally acknowledged as one of the leading groups for dating Mesozoic marine rocks; 6) it allows one to assess *a posteriori* and objectively, the diachronism of the studied taxa and to choose the actual characteristic taxa of each zone; and, last but not least, 7) Escarguel and Bucher (2004) demonstrated that the unknown duration of discrete biochronozones produced by the unitary association method does not involve *ceteris paribus*, a methodological bias when inferring temporal changes in taxonomic richness (an invaluable property for biodiversity analyses).

The unitary association method constructs zonations composed of a sequence of discrete, association zones, called UA-zones, which are maximal sets of intersecting ranges of taxa and the finest possible subdivisions from the association concept. Fundamentally, Opper Zones, Concurrent Range Zones, Assemblage Zones, and Unitary Associations Zones are closely related because they are all based on the coexistence of species. The UAM differs from other association methods in that it parsimoniously exploits conflicting biostratigraphic relationships that commonly occur among first occurrences (FOs) and last occurrences (LOs) of taxa, to infer virtual associations (i.e. coexistences in time but not in space). The reader should be aware that a strict association zone (such as those produced by the UAM) is characterized either by the taxa occurring only within this zone, or by the intersecting ranges of taxa observed within the zone. The UAM has been automated by the BioGraph computer program (Savary and Guex 1991, 1999). Edwards and Guex (1996) and Monnet and Bucher (2002) summarized the major princi-



TEXT-FIGURE 1

Location of studied areas (northwestern Nevada, British Columbia, and Sverdrup Basin). Middle Triassic paleogeographical map modified after Golonka and Ford (2000) and Stampfli and Borel (2002).

ples of this deterministic method. See Guex (1991), Angiolini and Bucher (1999) and Monnet and Bucher (2002) for an exhaustive methodological use of the UAM. Monnet and Bucher (1999, 2002) also developed an additional optimization procedure that automatically select for the best legal input data set in order to obtain more accurate results (a minimum number of remaining biostratigraphic contradictions and a maximum number of UA-zones). This latter approach is the method used throughout this study.

#### Correlation method

In order to avoid the pitfalls of diachronism and endemic taxa, the revised zonal sequences are correlated by creating a zonation, which considers all of the taxa common to the studied basins. This 'common taxa zonation' is achieved by utilizing the UAM in conjunction with the previously cited optimization procedure at both the species and genus levels. These 'common taxa zonations' make it possible to date each local zone (i.e. restricted to a basin) by determining which local zone documents the characteristic or age-diagnostic species and/or genera (singletons or pairs of intersecting ranges) of each global zone (at the scale of North America) of the common taxa zonation.

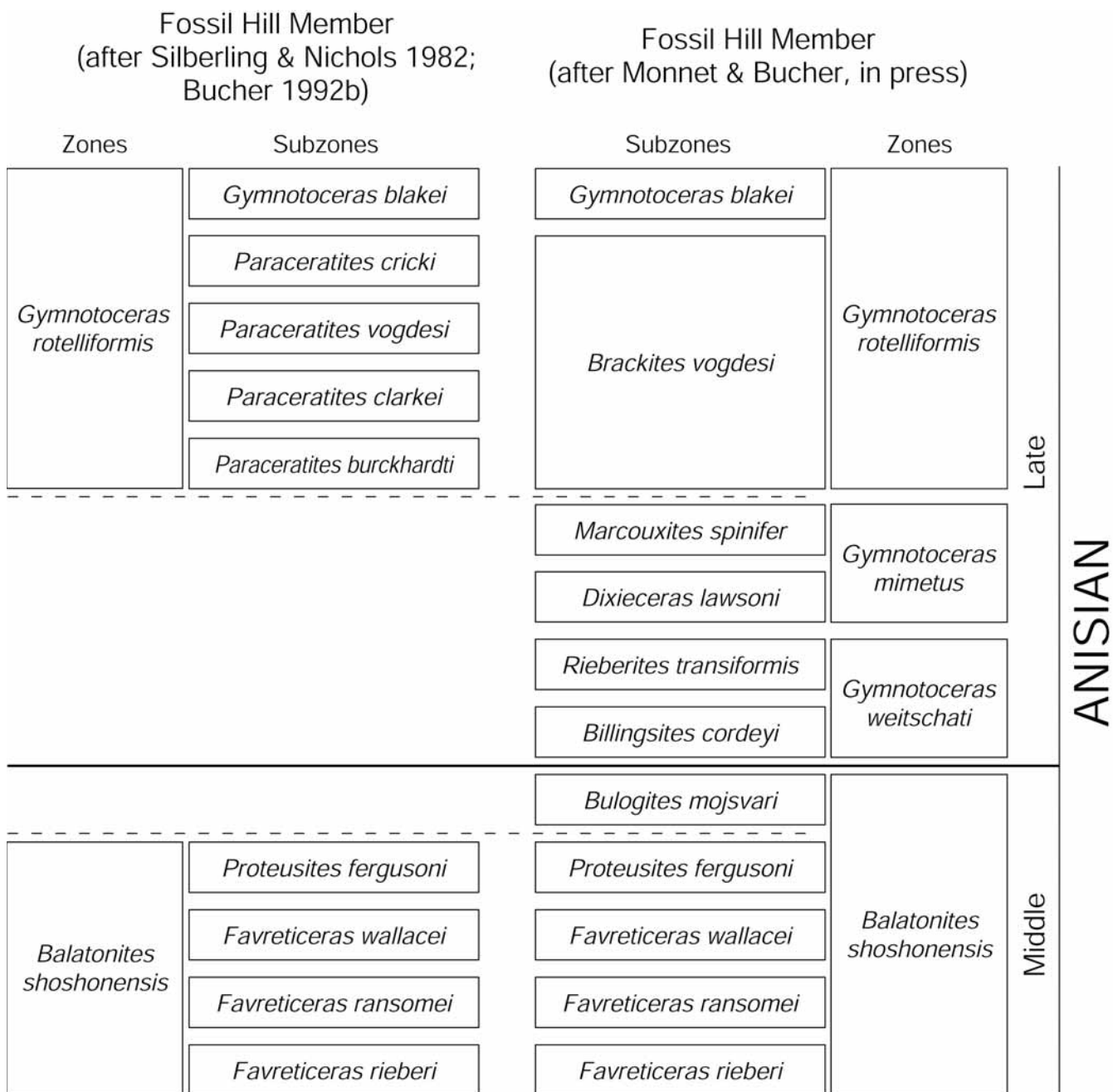
The interest of this approach is twofold. First, it enables one to be more objective and precise in correlating the studied areas.

Indeed, common taxa zonation allows for the correlation of local, basin-scaled zonations with greater confidence, because it is based on all of their common taxa rather than just a few taxa arbitrarily chosen as index guides. Hence, this method determines if a local zone is an exact correlative of another local zone, if it is correlative with a group of zones, or if it has no correlative at all in the other basin. Secondly, it makes it possible to assess the diachronism of the taxa common to the studied basins since it is usually not negligible and must be taken into account.

#### RESULTS

The zonal sequences are separately revised for each studied area by utilizing the unitary association method. The resulting data set contains 174, 90, and 7 species for the entire Anisian from Nevada, British Columbia and the Sverdrup Basin, respectively. Likewise, the three studied areas contain 13, 10, and 3 zones, respectively. The faunal content of each zone is listed in text-figure 4.

The results of this revision are congruent with the previous empirical zonations with the exception of the *Nevadites hyatti* Subzone of the Nevada *Frechites occidentalis* Zone, which is herein rejected because it does not have diagnostic taxa or association of taxa. Indeed, its entire faunal content is included within the more diverse *Nevadites humboldtensis* Subzone.



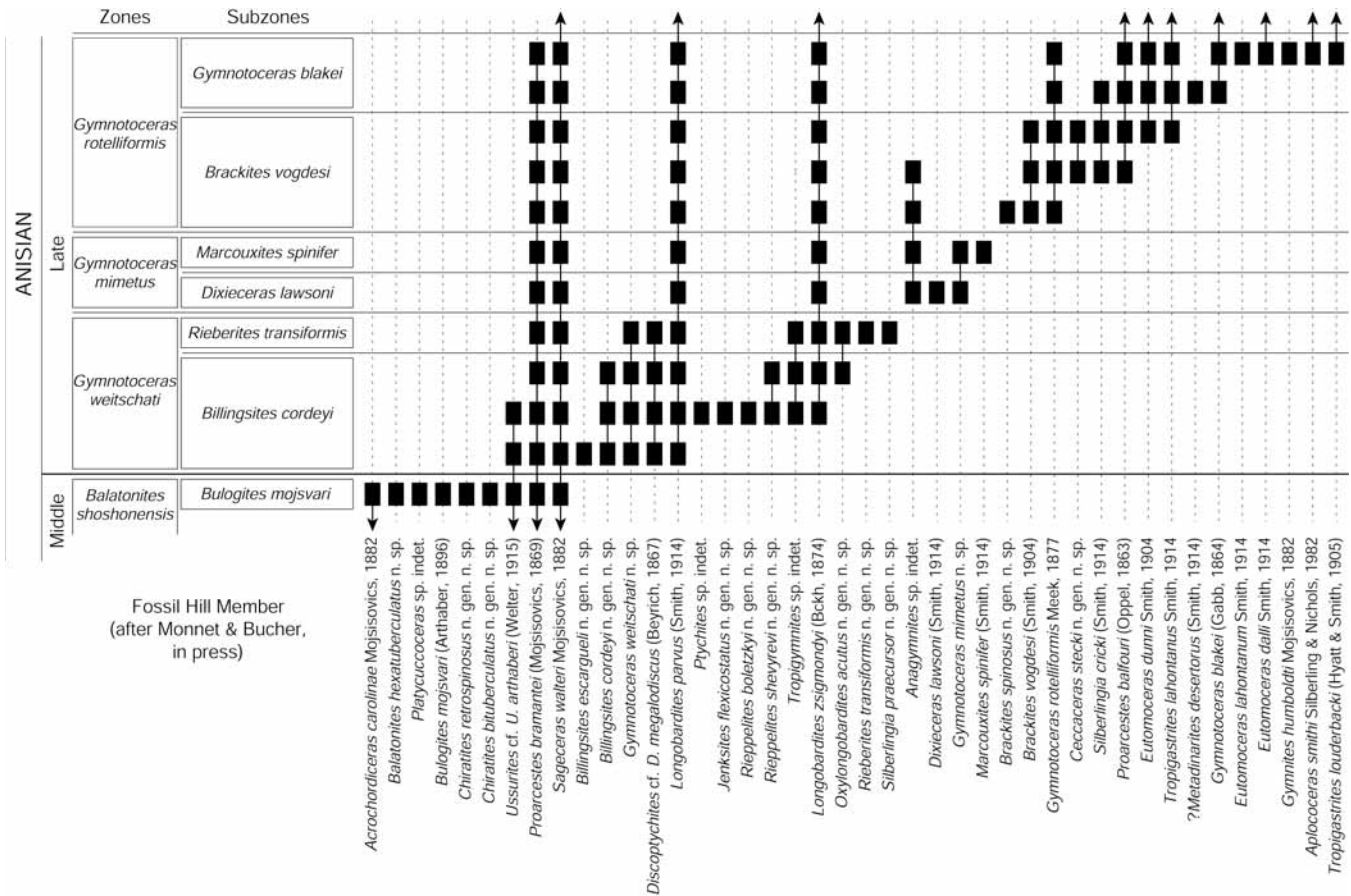
TEXT-FIGURE 2  
Revised ammonoid zonation of the Fossil Hill Member (Nevada) around the Middle/Late Anisian boundary (after Monnet and Bucher, in press).

Hence, the two subzones of the *occidentalis* Zone as defined by Silberling and Nichols (1982) are here merged.

The zonal sequences of Nevada, British Columbia and the Sverdrup Basin have been correlated by utilizing the ‘common taxa zonation’ as explained above. For example, the sequences for Nevada and British Columbia have been processed together as a two-section data set after taking into account all taxa (first species and then genera) common to the two basins. This yields a zonation consisting of six zones from 11 common species (text-fig. 5A), and 14 zones from 30 common genera (text-fig. 5B). For instance, in Nevada and British Columbia the *Para-*

*crochordiceras americanum* Zone contains the restricted occurrence of the genus *Columbisculites*, which constitutes a characteristic taxon of the ‘common-zone’ 4 (text-fig. 5B).

Based on these ‘common taxa zonations’, the resulting proposed correlation of the zonal sequences for Nevada, British Columbia and the Sverdrup Basin is displayed in text-figure 6. It is immediately apparent that the low-paleolatitude Nevada sequence contains by far the most complete succession of ammonoid faunas. Based on the present state of available data, all demonstrated correlations as well as all remaining uncertainties are graphically represented by the boxes in text-figure 6.



TEXT-FIGURE 3  
Synthetic range chart showing the biostratigraphic distribution of ammonoids around the Middle/Late Anisian boundary in the Fossil Hill Member (after Monnet and Bucher, in press).

Note that uncertainties in the correlations are portrayed by thick vertical black bars in text-figure 6. For instance, the *weitschati* Zone is documented neither in British Columbia, nor in the Sverdrup Basin. It is noteworthy that several local, basin-scaled zones do not contain the diagnostic faunas of the ‘common taxa zonations’. This uncertainty indicates either that the correlation remains indeterminate or that equivalent zones have not been documented in the other basins. As an example, the correlation of the *Tetsaoceras hayesi* Zone of British Columbia with the Nevada sequence is relatively uncertain. Nevertheless, this zone probably correlates with the *Unionvillites hadleyi* Subzone of Nevada, because among their common, non-diachronous datums both zones contain the index species *Tetsaoceras hayesi* and document the last occurrence of *Isculites tozeri* (see text-fig. 4). A zone of a particular basin may also correlate with several zones in the other basin. For instance, the *Lenotropites caurus* Zone of Nevada may equally correlate with the *Azarianites bufonis* and *Grambergia nahwisi* subzones of British Columbia because the characteristic species or pairs of species of the *caurus* Zone are found in these two subzones.

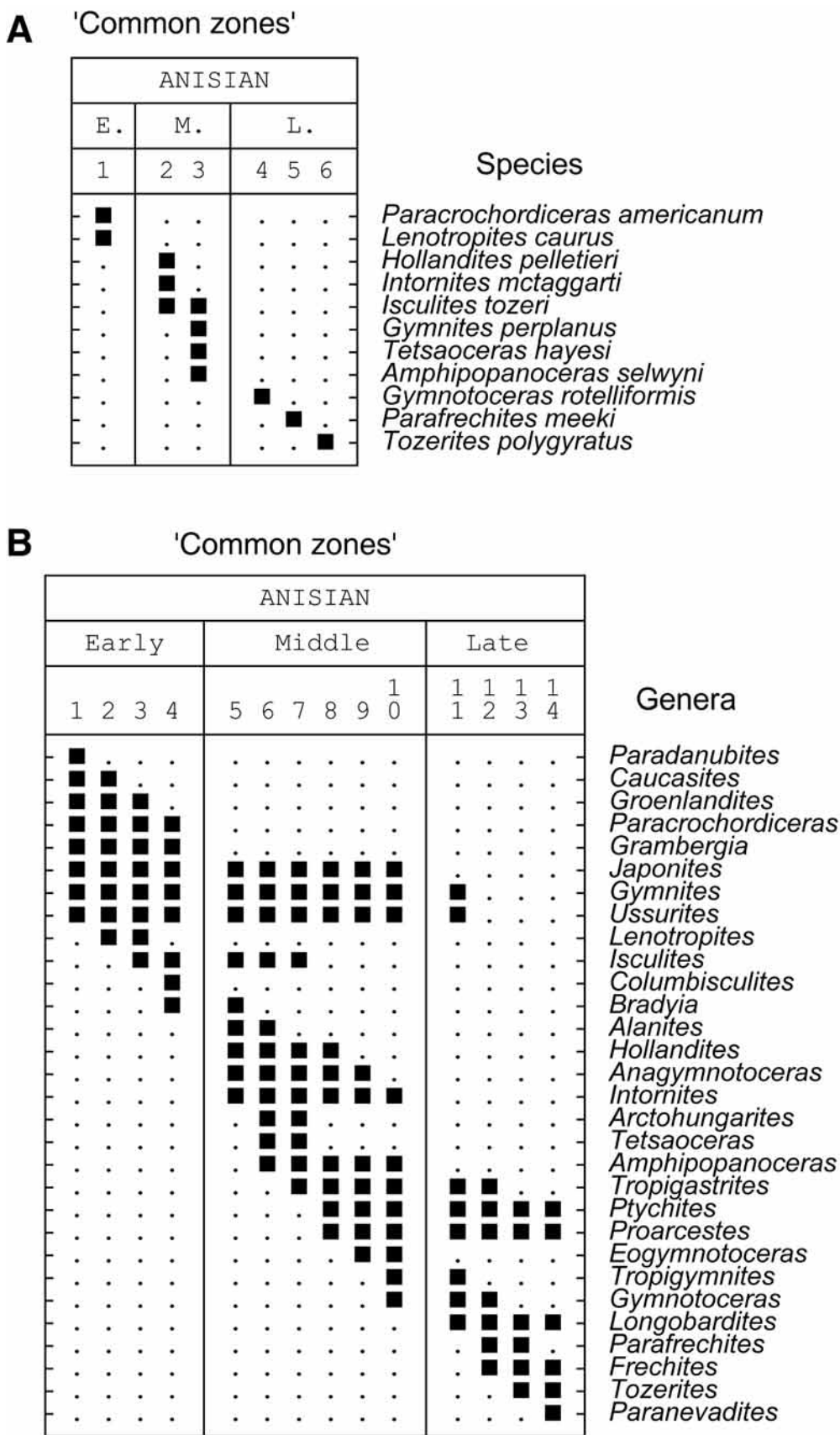
The correlations proposed here are at slight variance with those already published by other workers (e.g. Tozer 1994b: text-fig. 7). For instance, Tozer broadly correlates the *Buddhaites hagei* Zone with the *Acrochordiceras hyatti* Zone, whereas our work

indicates that the *hagei* Zone correlates more precisely with the *Intornites mctaggarti* Subzone of the *hyatti* Zone because of the common and exclusive occurrence of *Hollandites pelletieri*.

Our correlations also show two additional discrepancies with Tozer’s scheme. First, Tozer correlated the *hayesi* Zone with the *Nevadisculites taylori* Zone of Nevada, whereas it is herein correlated with the *hadleyi* Subzone of the *hyatti* Zone. This correlation is prompted by the coexistence of *Tetsaoceras hayesi* and *Gymnites perplanus* with the genus *Alanites*. Second, Tozer correlated the *Hollandites minor* Zone with the *shoshonensis* Zone of Nevada. We find that the *minor* Zone is in fact difficult to correlate with any degree of precision. The only species of the *minor* Zone in common with the Nevada sequence is *Amphipopanoceras selwyni*. This species is found in the *Favreticeras rieberi* Subzone of Nevada and in the *hayesi* Zone of British Columbia, which in turn correlates with the *hadleyi* Subzone of Nevada. Unfortunately, the genera common to Nevada and British Columbia in this zone are of no help because their ranges extend well beyond the zone. Therefore, the *minor* Zone is roughly equivalent to the *Pseudodanubites nicholsi-F. rieberi* interval of Nevada, which indicates that the *minor* Zone is more likely correlative with a part of the *taylori* Zone and not of the *shoshonensis* Zone as hypothesized by Tozer (1994b).

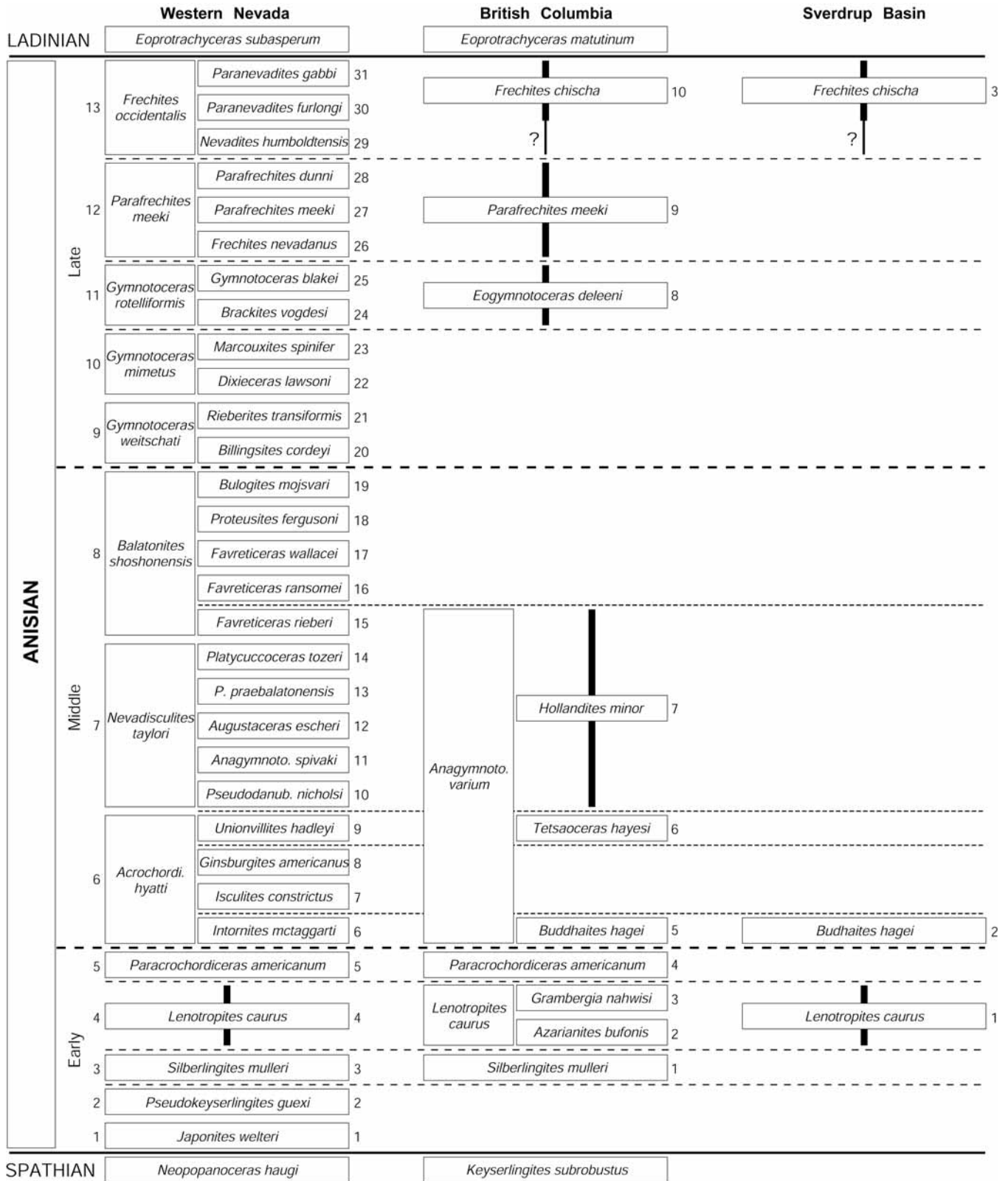






TEXT-FIGURE 5  
Common taxa zonations of Anisian ammonoids from Nevada and British Columbia at the species level [A] and genus level [B].





TEXT-FIGURE 6  
 New correlations of the ammonoid zonation of Nevada, British Columbia, and the Sverdrup Basin. Numbers on right refer to those of text-figure 4. Numbers on left refer to those of text-figure 8. Thick vertical black bars indicate poorly constrained correlations. The length of these black bars shows the maximal amount of uncertainty.

	Nevada	B. Columbia
ANISIAN	<i>F. occidentalis</i>	<i>F. chischa</i>
	<i>P. meeki</i>	
	<i>G. rotelliformis</i>	<i>E. deleeni</i>
	<i>B. shoshonensis</i>	<i>H. minor</i>
	<i>N. taylori</i>	<i>T. hayesi</i>
	<i>A. hyatti</i>	<i>B. hagei</i>
		<i>L. caurus</i>
	<i>S. mulleri</i>	

TEXT-FIGURE 7  
Correlation of Nevada and British Columbia ammonoid zones after Tozer (1994b). Note the position of the *minor* and *hayesi* Zones as compared to text-figure 6.

Finally, the revised zonations as well as their correlation with each other, reveal a significant amount of diachronous taxa for both first and last occurrences (~18% and ~67% of the common species and genera, respectively). Text-figure 8 clearly illustrates that few species and genera are actually synchronous. Whatever the cause(s) of this diachronism (e.g. preservation, paleobiogeographical, or paleoecological biases), this bias is still overlooked by a large number of ammonoid workers who persist in using the first appearance of index taxa for correlation.

### BIODIVERSITY

Several metrics are utilized to extract and analyze ammonoid biodiversity patterns. These include species richness, origination and extinction, turnover, and poly-cohort analysis. Monnet et al. (2003) described and discussed these biodiversity indices. The Sverdrup Basin is not included because of its highly discontinuous fossiliferous record and its highly depauperate faunas.

The species richness (number of species occurring within each zone) of both basins fluctuates greatly, starting with low values in the Early Anisian (text-fig. 9A, D). It reaches its highest values in the early Middle Anisian (*hadleyi/hayesi* subzones), and declines from then on to moderate values until the Anisian/Ladinian boundary. Text-figure 10 illustrates the percentage for each family for the entire stage in terms of its number of species, for each basin. British Columbia is dominated by Beyrichitinae among the Ceratitidae, Longobarditidae, and to a lesser extent by Gymnitidae and Parapopanoceratidae, while Nevada is almost completely dominated by Beyrichitinae and Paraceratitinae among the Ceratitidae, and to a lesser extent by Acrochordiceratidae, Balatonitidae, Gymnitidae, and Longobarditidae. It is noteworthy that the species richness of the Nevada subzones is nearly identical on average, to that of the British Columbia zones.

Originations (number of species appearing between two successive zones) and extinctions (number of species disappearing be-

tween two successive zones) have narrow fluctuations (text-fig. 9B, E) and are significant only at the Early/Middle Anisian boundary (peak of origination) and within the Middle Anisian at the *hyattitaylori* zone boundary (peak of extinction).

The turnover (sum of originations and extinctions) is relatively important, and indicates high evolutionary rates for the ammonoid faunas at that time (text-fig. 9C, F). Due to a lower resolution record, the Canadian turnover has higher values than does Nevada, but both basins have their highest turnover values at the Early/Middle Anisian boundary, at the *hyattitaylori* zone boundary within the Middle Anisian, and at the Middle/Late Anisian boundary. The Early/Middle Anisian boundary is marked by the diversification of Beyrichitinae, whereas the Middle/Late Anisian boundary is marked by the diversification of Paraceratitinae. Note that the Early Anisian of Nevada records the recovery of ammonoid faunas from the lowest values of species richness at the Spathian/Anisian boundary, and shows an increasing trend of species richness as well as the highest turnover percentages.

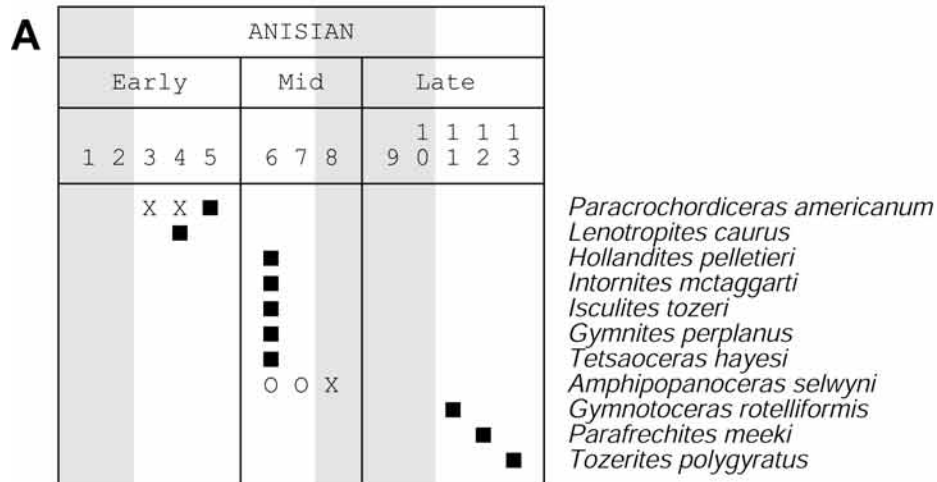
However, the biodiversity fluctuations described above are relatively weak. There are no statistically abnormal values in either basin that would indicate a particular significant event departing from background fluctuations. This is corroborated by the absence of significantly non log-linear poly-cohorts (results not illustrated here), which suggest the absence of a statistically significant extinction phase. More generally, a poly-cohort which fits a log-linear regression indicates relatively stable extinction rates through time (see detailed example in Monnet et al. 2003).

In conclusion, the Anisian ammonoid faunas of British Columbia and northwestern Nevada have no significant (departing from background) values of biodiversity (either common or not), which may indicate a period of relative stability for ammonoids. Nevertheless, the *hadleyi/hayesi* subzones (early Middle Anisian) record a peculiar paleobiogeographical event in addition to their very high species richness and turnover values as seen above. Indeed, it corresponds to a brief time interval during which exchanges did occur between latitudinally restricted faunas. For example, low paleolatitude genera such as *Pseudodanubites* and *Isculites* occurred briefly in British Columbia, while mid- and high paleolatitude genera such as *Arctohungarites*, *Amphipopanoceras*, and *Czekanowskites* expanded their ranges southward. This event may have resulted from brief but significant changes in climate or oceanic circulation.

Another noteworthy event occurred during the *caurus* Zone, which records the spread of typical Boreal faunas in Nevada. As already noted by Dagys (1988), during the Early Anisian longobarditids (*Groenlandites*, *Grambergia*), parapopanoceratids (*Stenopopanoceras*), and danubitids predominated in the Boreal realm, whereas ussuritids (*Ussurites*, *Monophyllites*), japonitids (*Japonites*, *Caucasites*), acrochordiceratids (*Paracrochordiceras*), and sturiids (*Sturia*) characterized the Tethyan realm. Text-figure 5B clearly shows that most of these Boreal genera also occurred in Nevada during the *caurus* Zone. This southward migration of Boreal ammonoids may reflect a cooling event.

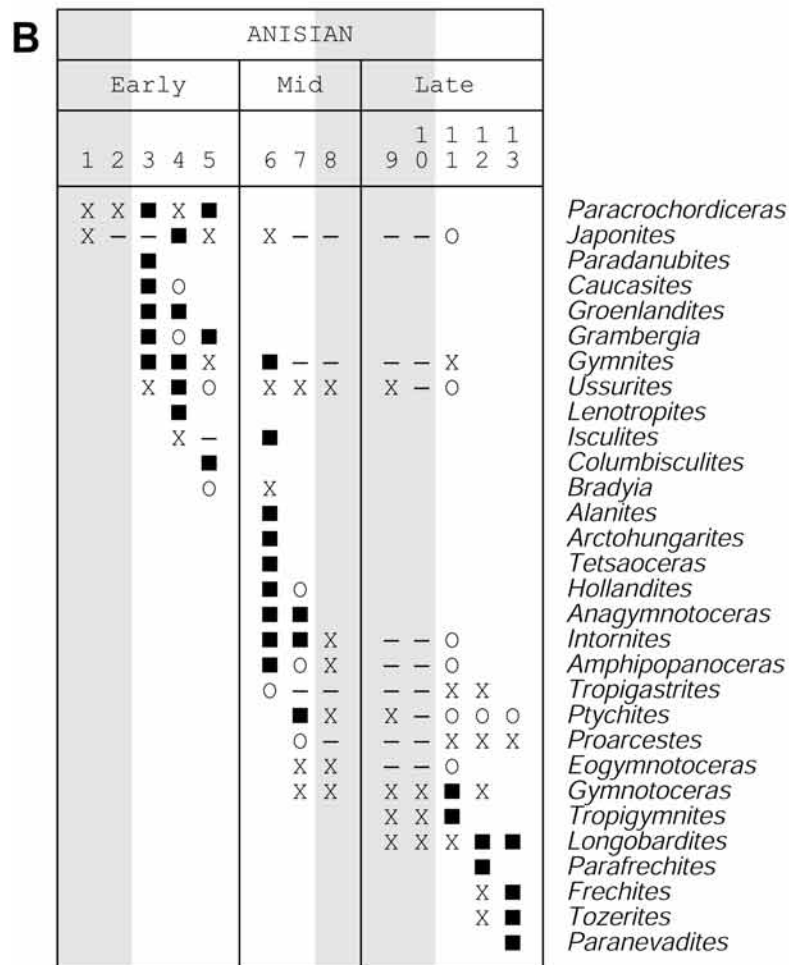
### CONCLUSIONS

This study synthesizes and revises the zonal sequences as well as their correlation with each other for three basins situated

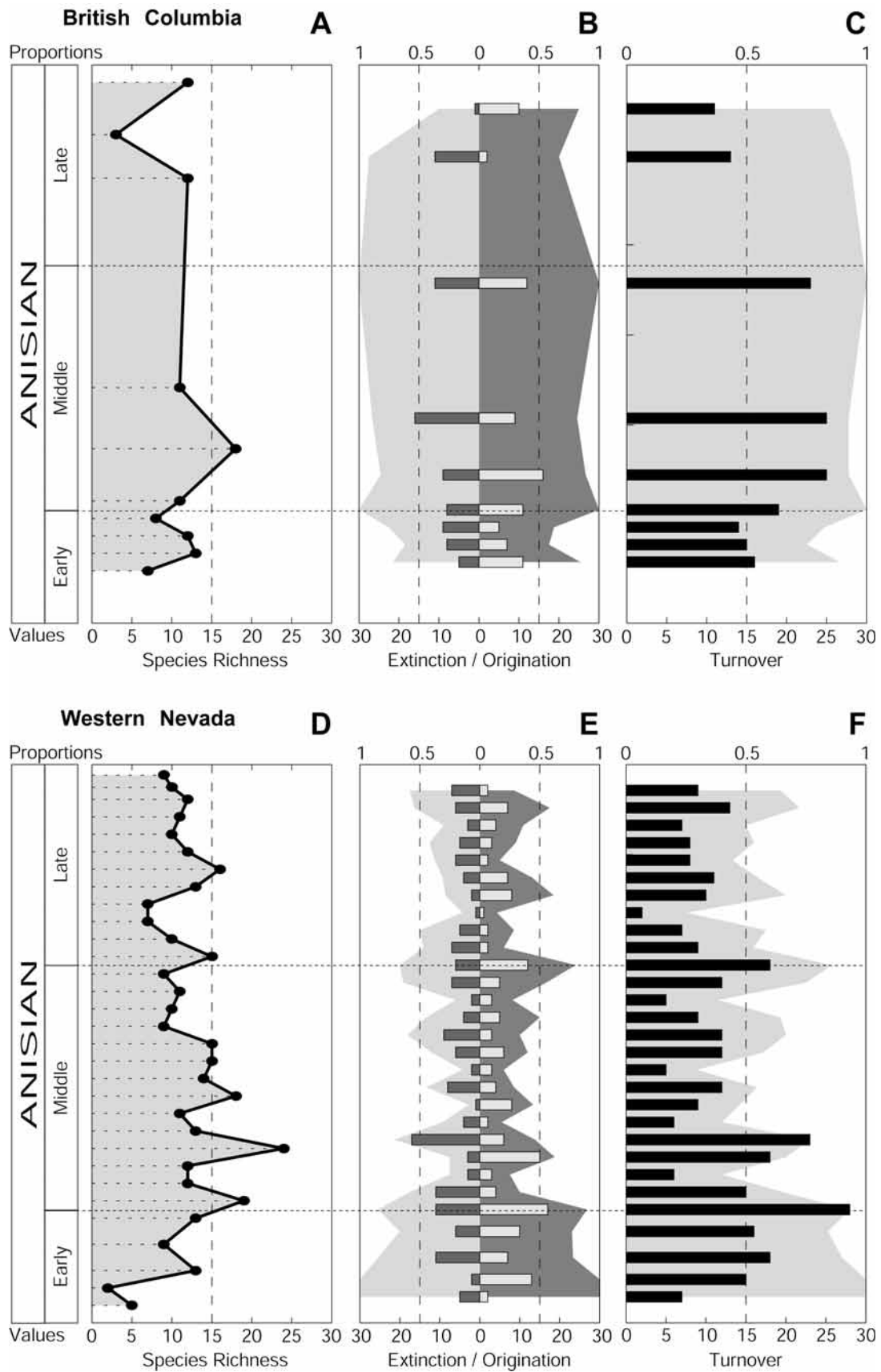


X -> Nevada  
 O -> British Columbia  
 ■ -> Ne & BC

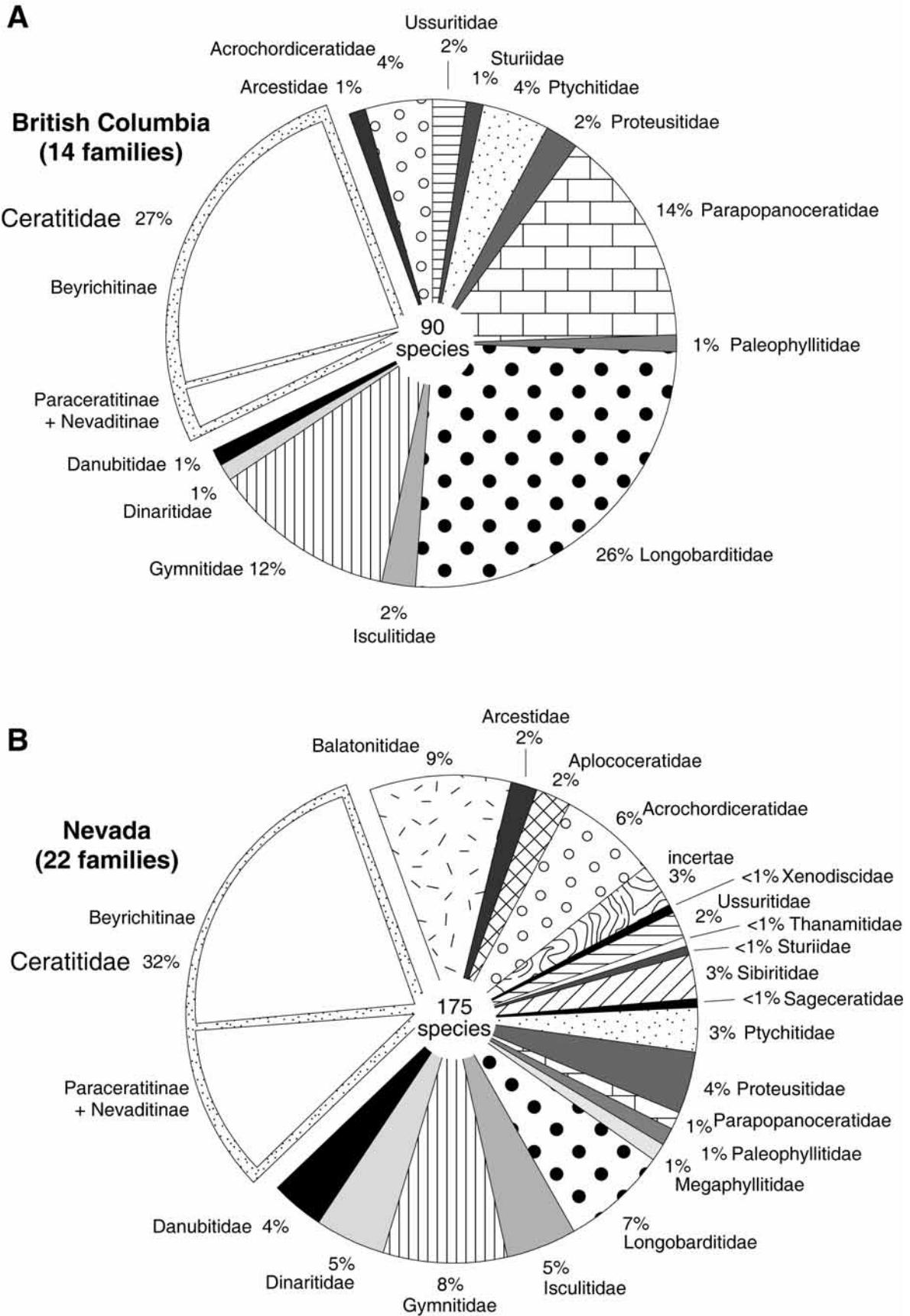
- genus or species unknown within the zone



TEXT-FIGURE 8  
 Biostratigraphic ranges and diachronism (at the zonal level and in terms of both first and last occurrences) of Anisian ammonoids from Nevada and British Columbia at the species level [A] and genus level [B]. See text-figure 6 for zone numbers. Shaded areas indicate documentation gaps in British Columbia.



TEXT-FIGURE 9  
 Diversity changes of ammonoids during the Anisian stage in British Columbia and Nevada. [A, D]: species richness values. [B, E]: extinction/origination values (bars) and percentages (shaded areas). [C, F]: turnover values (bars) and percentages (shaded area).



TEXT-FIGURE 10  
 Percentage of each Anisian family (number of species) for British Columbia [A] and Nevada [B].

along a paleolatitude gradient in the North American Cordillera (Nevada, British Columbia, and the Sverdrup Basin). The zonations are constructed by utilizing the unitary association method, which constructs discrete, association zones. Based on a standardized taxonomy, the studied areas contain 13, 10, and 3 zones and 174, 90, and 7 species, respectively. The construction of a global zonation based on all taxa common to the studied basins (common taxa zonation) leads to more precise correlations, which are at slight variance with the 'standard' correlations of the literature, such as those of Tozer (1994b). Indeed, the *hagei* Zone (Canada) correlates only with the *mctagarti* Subzone (Nevada) rather than the entire *hyatti* Zone (Nevada), and the *hayesi* Zone (Canada) appears to correlate with the *hadleyi* Subzone (Nevada) of the *hyatti* Zone rather than the *taylori* Zone. The *minor* Zone (Canada) more than likely correlates with the *taylori* Zone (Nevada) rather than the *shoshonensis* Zone, as is usually acknowledged. The unitary association method, utilized for this biochronological revision, enables one to objectively and *a posteriori* quantify the amount of diachronism of the studied taxa. Consequently, this study reveals that 67% of the 30 genera common to Nevada and British Columbia are diachronous for both first and last occurrences. Finally, these revised zonations provide a robust time frame for diversity analyses. It demonstrates that species richness peaked during the Nevada *hadleyi* Subzone (early Middle Anisian), which obviously represents short-term migrations between normally latitudinally restricted faunas. This event may reflect significant changes in climate or in oceanic circulation at that time.

It is also noteworthy that the species richness values for the Nevada subzones are nearly identical on average to those of the British Columbia zones. Although this pattern may partly reflect a preservation bias resulting from the reduced carbonate content of the higher latitude record, it nevertheless does not exclude lower speciation rates among higher latitude taxa. Species counts derived from single horizons of early diagenetic carbonate nodules in the high latitude record (British Columbia, Sverdrup Basin) do actually provide a reliable measure of species richness.

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