#### REVIEW

# An interim global bioregionalisation of Devonian areas

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# Abstract

We present an interim Devonian bioregionalisation in which previous zoogeographical and biogeographical areas of Devonian taxa are reviewed. This review has been long overdue, as Devonian bioregionalisation has become poorly constrained since the foundational work of Arthur J. Boucot in the late 1960s. A systematic review of over 100 areas and amendments is completed for the first time with addition of three new areas: the Mardoowarra and the Late Devonian Eastern Australasia region, and Western Gondwana realm. This interim regionalisation is the first to be completed and standardised, made in preparation for future palaeobiogeographic studies and as a prelude to rigorous testing. By standardising the 1969 bioregionalisation of Boucot et al. Devonian biogeography can begin to assess if the proposed bioregionalisation is representative of true natural areas.

Keywords Area nomenclature · Biogeography · Eastern Americas · Malvinokaffric · Old World · Palaeobiogeography

### Introduction

Multi-taxon global bioregionalisations have been the backbone of both biogeographic (Sclater 1858; Wallace 1876) and palaeobiogeographic studies (Arldt 1907; Schuchert, 1909). The descriptions of areas and their nomenclature (sensu Wallace 1894; Arldt 1912) have been vital to maintaining existing bioregionalisations, reducing the number of conflicting terms and descriptions. While these practises were prevalent in the early twentieth century, they have become neglected after the 1960s. The modern single-taxon global bioregionalisations appropriate terms from previous multi-taxon approaches, resulting in numerous revisions of areas such as 'Gondwana' and 'Australasia'. Devonian bioregionalisation had also suffered the same fate.

Arthur J. Boucot (1924–2017), established the framework for a hierarchical global Devonian area classification shortly after the plate tectonic revolution of the 1960s (Boucot et al., 1969). After the presentation and revisions of Boucot's work, Devonian bioregionalisation became an active field with a plethora of authors challenging (Bowman Bailey, 1978; Kobayashi and Hamada 1975; Young, 1981, 1986) or supplementing Boucot's original regions (Hou, 1981; Bigey 1985; Blodgett et al., 1990; Afanasieva and Amon, 2013; amongst others). Additionally, the bioregionalisation of Boucot et al. (1969) despite its revisions and amendments has never been completed with areas left unassigned. This incomplete bioregionalisation, without any checks on the use of names or their definitions, has been foundational in many subsequent biogeographic studies. Consequently, this has led to a confusing set of single-taxon bioregionalisations and unstable *area taxonomy* (a hierarchical classification of names see Ebach and Michaux 2017).

This paper aims to review and standardise global marine Devonian bioregionalisation into single, interim area taxonomy for use in future bioregionalisation studies.

# A practitioner driven field

Bioregionalisations and area classifications have been a feature of the natural sciences since the nineteenth century. The consideration of bioregionalisation and taxic distributions have proven a key tool for palaeoreconstructions and instrumental in the development of geological theories such as continental drift. Prior to Boucot, palaeogeographers characterised areas using unranked and unstructured terms such as geographical realms (e.g. Old World, Old Red Continent), geological distributions (e.g. basins, formations, assemblages), or the continents themselves (e.g. North America, Gondwana,



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Lemuria, Archiplata; see Suess, 1885; von Ihering, 1892; Schuchert, 1903, 1909).

Most notable in raising the issue of nomenclature was Anthony Hallam who remarked that "of the older literature bearing on past continental relationships, as summarised for instance by Arldt (1919-1921), has required or still requires critical revision in the light of modern knowledge and the more rigorous standards of today" (Hallam, 1966, p. 204).

Although Hallam was commenting on bioregionalisation in general, the framework for a formal Devonian area classification is largely due to Boucot (Boucot et al., 1969; Boucot and Gray, 1974; Boucot, 1985, 1988, 1993; Boucot and Blodgett, 2001; Boucot et al., 2008). Boucot used overlapping distributions constrained by geological and geographical features to delineate his areas and brought structure to the nascent field. However, relics of prior approaches remained within his work, for instance the use of 'Old World' (e.g. *Orbis Terrarum Veteribus* Jansson 1650; *Orbis Vetus* Sanson 1657), a cartographical term used to describe Europe, Africa and Asia goes back to seventeenth century after the discovery of the New World (North and South America). Consequently, Boucot's areas are open to scrutiny.

Kobayashi and Hamada (1975), abandoned the idea of the Old World, while others remained in favour (Chlupac, 1975; Cocks and McKerrow, 1973; Bigey, 1985; Blodgett et al., 1990; Hallam, 1994). Further discoveries of taxa and their distributions led to areas being added and subtracted in any given bioregionalisation. For example, two of the three realms proposed by Boucot et al. (1969), the Eastern Americas and Malvinokaffric realms were eliminated or reduced in the Late Devonian, resulting in two equally unlikely eventualities: (1) either the Old World realm was global in distribution (an impossibility due to its shallow, warm-water characteristics) or (2) that despite the maintenance of regions and provinces, those outside of the bounds of the Old World realm existed within an undefined, unranked area. To assist in the resolution of this problem, three new areas have been proposed to complete the bioregionalisation of the Late Devonian.

Though the bioregionalisation of Boucot et al. (1969) has be reconsidered by various authors using alternate taxa (such as Kobayashi and Hamada, 1975), it remains the standard by convention amongst palaeobiogeographers. As a consequence, alternative bioregionalisations not considered here. With over 100 biotic areas named since Boucot's framework was established, we feel it is timely to systematically review known Devonian biotic areas including the stratigraphic range, distribution and diagnosis of realms, regions and provinces. The following systematic review is in character with Boucot's original classification, although several ranks have been recast to form a more stable bioregionalisation (Table 1). Each area of realm, region or province rank will be given a standardised nomenclature, reviewed and their subprovinces listed.

#### A note on area nomenclature

The stability of any area taxonomy lies in the strength of its nomenclature. Since Boucot et al. (1969), the competing nomenclature of authors has seen variability in biogeographic taxonomic rank. For instance, compare the New Zealand region (Boucot and Gray, 1979) and the New Zealand province (Young, 1981), or the Malvinokaffric realm (Oliver, 1977) and the Malvinokaffric province (Boucot et al., 1969) and the confusion in comparing ranks both spatially and temporally. Despite the few attempts to establish a formal biogeographic nomenclature (e.g. Cecca and Westermann, 2003; Ebach et al., 2008; Servais et al., 2013), very few authors describe their process for establishing hierarchy and even fewer justify new area names (e.g. Lebedev and Zakharenko, 2010) or reasons for the maintenance of Boucot's original hierarchy across differing taxa (Oliver, 1977; Bigey, 1985 amongst others).

For the purpose of this study the *International Code of Area Nomenclature* (ICAN) (Ebach et al., 2008) will be applied to all biogeographical areas as it makes the least number of assumptions concerning area definition and focuses on area nomenclature, rather than on ecological history or, evolutionary, ecological or biogeographic processes (sensu biochores/ bichorema, Westermann, 2000; Yanin, 2010; Servais et al., 2010). To formalise each named area, the ICAN requires area names to be designated a name-bearing type locality and a diagnosis, in which areas may be synonymised. The types are taken from the studies that established the biogeographic area. Types will be the formation, group, series, or basin at higher ranks, within which are found the characterising taxa. If the author(s) of the original studies do not provide a locality, selection was made by using the same approach.

The ICAN is vital for preserving names and acknowledging synonymies. The ICAN has been used extensively in extant bioregionalisations across various phyla (Albert and Reis, 2011; López et al., 2008; Lumbantobing, 2010; Escalante et al., 2013; Costa et al., 2013; Neubauer et al., 2015; Van Rooy and Van Wyk, 2010; Postigo Mijarra et al., 2009; Ebach et al., 2013, 2015; Morrone, 2014, 2015a,b). The usage of the term 'region' is an exception, for though it is considered by Cecca and Westerman (2003) to be 'informal', within the ICAN 'region' is considered a rank above 'province' and one rank below 'realm'.

#### Ambiguous names and concepts

#### Zoogeography

The zoogeographic practise of naming areas after their characterising taxa (for example, the Sinogaleaspid-Xiushuiaspid realm of Pan and Dineley, 1988) does not allow for standardisation. Biogeographic areas are established based upon the shared distributions of multiple taxa (sensu area of

Realm	Region	Province	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennia
Eastern America									
	N/A	Appohimchi							
		Nevada							
		Michigan Basin	1						
		Venezuela-Colombia							
Malvinokaffric	N/A								
Old World	I								
	Cordilleran			_	_	_	_	_	_
		Alaska-Yukon	-						
		Euramerican							
		Western Canada				)			
		Nevada				)			
		Mackenzie			_	)			
	Eastern Austra	alasia	1						
	New Zealand			_		)			
	Rhenish-Bohe	Rhenish-Bohemian							
		North Africa							
	Tasman								
		East Australia							
	Mardoowarra								
	South China								
		Junggar-Xinan							
		South China							
	Uralian								
		Balkash-Mongolo-Okhotsk				)			
		Siberian							
		Ural-Southern Tianshan							
		Tuva				)			

# Table 1 The ages of realms, regions and provinces within the Devonian

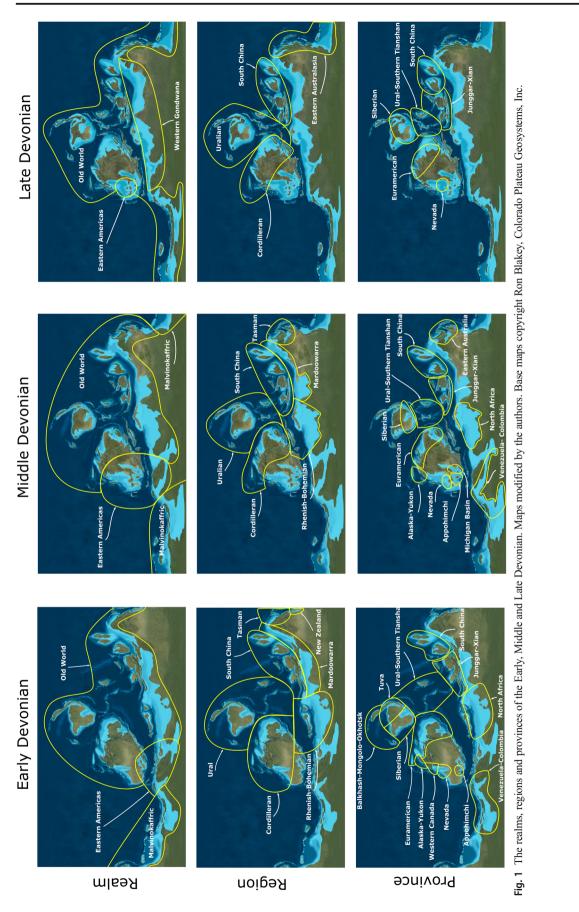
endemism; reviewed in Parenti and Ebach 2009). The use of characterising organisms as area nomenclature encourages the alteration of area names when the 'typifying' taxa decreases its influence or is replaced.

# Phytogeography

Devonian plant biogeography (phytogeography) is an underrepresented aspect of the field. Some Devonian phytogeography related instead the distribution of characteristics (Raymond, 1987) or were indeterminate in their characterisation (Hart 1976). Furthermore, studies in phytogeography (Edwards (1973, 1990) Streel et al., 1990, Rowley et al. (1985) Steemans et al., 2007, de Pasquo et al. 2009, Berry et al. 2000 amongst others) rarely engage with the marine regionalisations of Boucot et al. (1969) and would require their own review of bioregionalisation. As a consequence phytogeographic regions are omitted from this review.

# On the exclusion of planktonic areas

Afanasieva and Amon (2013) published a comprehensive analysis of Devonian radiolarian distributions and established four provinces and six subprovinces. The incompatibility of planktonic distributions with other faunal groups has been acknowledged by Afansieva and Amon (2013). As a consequence, their bioregionalisation, along with those on other planktonic organism such as by Klapper (1975), Fahraeus (1976) and Klapper and Johnson (1980), has been omitted from the review, used instead as supporting evidence.



# Systematic review of Devonian areas

#### Area taxonomic note

The interim area taxonomy herein (Table 1) adheres to the conventions of a systematic palaeontology with the following hierarchy outlined in the ICAN: realms, regions, provinces and subprovinces. All areas with the exception of subprovinces have a name, synonymy, stratigraphic range, type and diagnosis. As in a biological taxonomy, the diagnosis is purely descriptive. A remarks section is provided to summarise any existing biogeographic syntheses or hypothesis. The regionalisation is mapped according to Devonian age (Fig. 1).

# Eastern Americas realm

Appalachian province Boucot et al., 1969 Eastern Americas realm Boucot, 1974 Appalachian province Hou, 1981

Stratigraphic range: Early Silurian–Carboniferous (Boucot et al., 1980; Bigey, 1985; Oliver, 1990; Li, 2010).

**Type:** Appalachian Basin; New York, Pennsylvania, eastern Ohio, West Virginia, western Maryland, eastern Kentucky, western Virginia, eastern Tennessee, northwestern Georgia and northeastern Alabama.

**Diagnosis:** Warm-water unit with a highly endemic fauna such as the gastropods *Pleuronotus*, *Trochonema* (*Trochonemopsis*), *Elasmonema*, *Isonema*, *Turbonopsis*, *Palaeotochus*, spinose platyceratids, *Protolptosrophia* and *Plicoplasia* (Blodgett et al., 1990; Hallam, 1994). Silurian holdovers are considered unimportant within the Eastern Americas realm, though some are identified in the Appalachian Basin during the Gedinnian (Hallam, 1994). Extends to include areas south of the Central Canadian Shield (i.e. Michigan and Appalachian Basins, Venezuela and Colombia) and much of North America east of the transcontinental arch (Boucot, 1974; Boucot et al., 1980; Oliver, 1990; le Herisse et al., 1997).

A warm-water unit with connection, via a surface current, to the Malvinokaffric boundary in NW Argentina (Boucot et al., 1980). The border shared with the Malvinokaffric is positioned midway between the southern margin of the Amazon Basin, passing through the Parnaiba basin, and the northern margin of the Parana Basin (Boucot et al., 2001). During the Devonian the unit was seen as the intermediate between the Malvinokaffric and the Old World realms (Boucot, 1974; Wang et al., 1984). **Remarks:** During most of the Early and Middle Devonian the Eastern Americas realm was bordered by land on three sides; the cycles of regression and transgression that existed throughout the Devonian rendering the barriers to dispersal periodically ineffectual (Oliver, 1976; Li, 2010). The reduction of the surrounding barriers saw Lochkovian connections to the Great Basin, resulting in Old World elements within the brachiopod assemblages of Chihuahua Mexico (Oliver, 1976).

The Eastern Americas realm could not be differentiated from the Old World realm during the Eifelian, coincident with the Emsian transgression and increasing cosmopolitanism of the Eifelian (Li, 2010). Oliver (1990) noted the disintegration of provinces (based on rugose corals) was delayed until the Frasnian, when the realm ends transitioning into more cosmopolitan forms. However, the strict delineation of the realm requires reconsideration. Problems of the Eastern Americas realm's area nomenclature include the lack of clarification from authors regarding the upper or lower limits of each area proposed, also provinces and subprovinces are often used interchangeably (e.g. compare Boucot, 1974; Oliver, 1990; Li, 2010). In addition, Oliver (1977, 1990) is consistent in his use of terms (e.g. basins and areas with the same endemic fauna remain as provinces).

Warm-water incursions into the Eastern Americas realm from the Cordilleran region during the Kačák event may have increased Old World realm transport into the Appalachian, Michigan and Iowa Basins and to a lesser extent the Wabash Platform area (i.e. Ohio and South East Indiana in the US) (DeSantis and Brett, 2011). Original designations saw the Eastern America realm terminate in the Eifelian; however, the Nevada province maintained a distinctive element into the Late Devonian and to avoid an incomplete bioregionalisation, the realm's duration has been extended.

Appohimchi province

Appohimchi province Oliver, 1977

**Stratigraphic range:** Lochkovian to Frasnian (Oliver, 1990; Boucot and Blodgett, 2001).

**Type:** Onondaga formation, Eifelian (Bigey, 1985), New York State to Maryland.

**Diagnosis:** Warm-water fauna with significant coral diversity including Heterophrentidae, Zaphrentidae and Craspedophyllidae amongst others (Oliver, 1990). During the Lochkovian to the Eifelian, the area was distributed across Eastern North America and became restricted to the Appalachian belt from the Eifelian to the Frasnian (Oliver, 1990). **Remarks:** Taxa used for differentiation were not observed within the proximal basins and provinces of the Eastern Americas realm, though there was strong evidence for some faunal exchange between the basins of the Eastern Americas realm during the Emsian and subsequent transgressive cycles. Emsian Old World affinities were observed within the geographical area of the Appohimchi province by Amsden et al. (1968) and Ormiston (1968) (see Oliver, 1977).

# Nevada province

Nevadan subprovince Boucot et al., 1969

Nevada province Oliver, 1977 Great Basin province Pedder and Murphy, 2004

**Stratigraphic range:** Middle Devonian (Oliver 1990, Boucot and Blodgett, 2001; Pedder and Murphy, 2004).

**Type:** The Great Basin, including Nevada, eastern Oregon, southern Idaho and the Colorado River watershed (including the Las Vegas metropolitan area and the northwest corner of Arizona.

**Diagnosis:** A warm-water unit that underwent deepening due to the west to east transgression over the Transcontinental arch (Blakey, 2008). The platform, on shore peripheral fauna (Bigey, 1985) including the brachiopods *Megakozlowskiella*, *Leptocoelia*, *Pleiopleurina*, *Levenea*, *Acrospirifer*, *Echinocoelia* and *Costispirifer*. For faunal list, see Oliver (1990) and Boucot et al. (1969). Despite being distributed primarily across the Great Basin (southwest North America), the area of Western North America was annexed into the Eastern Americas realm during the lower Early and Middle Devonian (Oliver, 1990).

**Remarks:** Significant faunal exchange between the Appalachian province and the Old World realm saw the Great Basin annexed into the Eastern Americas realm during the Middle Devonian. The Great Basin was highly endemic, specifically seen within benthic fauna, allowing significant differentiation from the adjoining Western North America (Oliver, 1990). In the Early Devonian, the genera of the Great Basin were of Appalachian affinity but expressed divergence at the species level (Boucot et al., 1969).

# Michigan Basin province

Michigan Basin province Olivier, 1990

**Stratigraphic range:** Early Eifelian to late Givetian (Oliver, 1990).

**Type:** Michigan and Hudson Bay Basins including Illinois, Iowa (Oliver, 1990).

**Diagnosis:** Coral fauna including *Acrophyllum*, *Argutastrea*, *Hexagonia* (see Oliver, 1990 for full list) and the presence of Appohimchi coral fauna (Bethanyphyllidae). Distributed across the Michigan and Hudson Bay Basins including Illinois and Iowa (Oliver, 1990).

**Remarks:** Separated from the Appohimchi province at the start of the Eifelian coincident with the end of a transgressive stage. Unique identity defined despite significant Appalachian influence within the province (Johnson et al., 1985; Oliver, 1990).

**Subprovinces:** Michigan Basin-Hudson bay subprovince (Boucot and Blodgett, 2001).

# Venezuela-Colombia province

Venezuelan-Colombian province Oliver, 1977

**Stratigraphic range:** Early Devonian to early Givetian (Oliver and Pedder, 1989; Oliver, 1990).

Type: Rio Cachiri Group, Venezuela.

**Diagnosis:** Warm-water unit of Western European affinities and significant coral assemblages including *Bowenelasma*, *Cylindrophyllum* and affinity with Eastern North America corals in the Eifelian (Oliver, 1977). Few fenestellids were recorded from the Venezuelan Rio Cachiri Group with diverse bryozoan assemblages observed in Colombia's eastern Cordillera including fenestellids, ptilodictyids and fistuliporids from the Floresta Formation (Bigey, 1985). The unit was distributed across the Colombian-Venezuelan Basin. **Remarks:** Corals were rare in the surrounding area but persisted within the province (Oliver, 1977). The area is considered an extension of the Appohimchi province into northern South America and recognition of *Bowenelasma* in New York, Northern America (Oliver, 1990).

**Subprovinces:** Amazon-Colombian subprovince, the latter of which was subsequently split into the Amazon and Colombian subprovinces (Boucot and Blodgett, 2001; see Pedder and Murphy, 2004). Colombian subprovince Early-Middle Devonian (Boucot and Blodgett, 2001,). Amazon subprovince Early -Middle Devonian (Boucot and Blodgett, 2001).

# Malvinokaffric realm

Malvinocaffrische province Richter, 1941 Malvinokaffric province Boucot et al., 1969 Austral realm Chlupac, 1975 Malvinokaffric province Kobayashi and Hamada, 1975 Malvinokaffric realm Johnson and Boucot, 1973 Malvinokaffric realm Blodgett et al., 1990 Malvinokaffric province Anderson et al., 1999

**Stratigraphic range:** Early Devonian, with decline beginning in the late Emsian (Boucot et al. 1969) and final termination in the Givetian (Hallam, 1994; Holmquist 2008; Cocks, 2011; Aboussalam and Becker, 2011, de Melo, 1988).

**Type:** Chapada group, Paraná Basin from Mato Grosso to Rio Grande do Sul states, Brazil (Bosetti et al., 2011; Becker-Kerber et al., 2017).

**Diagnosis:** Restricted low diversity, often cold, deep-water faunas within dark terrigenous clastic lithofacies with detrital, unweathered mica lacking warm weather indicators (Boucot, 1984; Meyerhoff et al., 1996). Arctic to temperate climate but without glaciation, few corals, comparatively depauperate but with endemic brachiopod genus *Australostrophia* and a dominant *Orbiculoidea falklandensis* and homonalotid trilobite (*Burmeisteria*) presence across the realm (Oliver, 1977;

Copper, 1998; Boucot et al., 2001). Typical brachiopod genera include *Scaphiocoelia*, *Pleurothyrella*, *Notiochonetes*, *Tanerhynchia*, *Australispirifer*, *Notiochonetes*, *Australocoelia*, *Pleurothyrella* and an endemic species of *Schellwienlla* (Boucot et al., 1969; Cocks 2011). Trilobite fauna include Phacopinae, Calmoniinae, Acastavinae and Asteropyginae with endemic species of the Homalonotidae (Kobayashi and Hamada, 1975). The Bokkeveld series is considered Malvinokaffric based upon fish fauna such as *Machaeracanthus* and chondrichthyans (Young, 1987; Long et al., 1988; Anderson et al., 1999).

Boucot et al., 1969first identified the realm (then province) to include South America, southernmost Africa and Antarctica. During the Early Devonian the Malvinokaffric included West Africa from Ghana to South Africa, Antarctica, South America south from Lake Titicaca region and Matto Grosso south (Boucot et al., 1969; Boucot, 1985; Oliver 1990; Hallam, 1994). Remarks: The Devonian Malvinokaffric realm is believed to have originated from the Appalachian basin in the Silurian (Koch and Boucot, 1982; Hallam, 1994). The Silurian Malvinokaffric, one of the two predominant Silurian realms, provided no taxonomic continuity to that of the Devonian due to the terminal Silurian extinction (Berry and Boucot, 1970, Boucot, 1985; Hallam, 1994; Meyerhoff et al., 1996; Blodgett and Stanley, 2008). Chlupac (1975) noted the trilobite Phacops (Phacopina) was present within both the Malvinokaffric and Eastern Americas realm, though in low diversity and high abundance within the former realm. Interestingly, by the Lower Devonian, no Malvinokaffric realm brachiopods were observed within the Eastern American realm (Boucot et al., 2001). Transport between the realms was apparently one way with Eastern America realm brachiopods (Australocoelia, Australospirifer and Plicoplasia) present within the Malvinokaffric realm (Oliver, 1990; Boucot and Blodgett, 2001; Li, 2010).

Due to the cold water of the Malvinokaffric realm bryozoans, corals, conodonts, calcareous algae, nautiloids, stromatoporoids, bioherms and the significant brachiopod taxa *Atrypida* and *Gypidula* were notably absent (Oliver, 1977, 1990; Koch and Boucot, 1982; Meyerhoff et al., 1996; Hallam, 1994; Boucot et al., 2001). Gastropod diversity was lowest within the Malvinokaffric realm, absent within the Lochkovian, emerging within the Pragian and Emsian and absent by the Givetian (Blodgett et al., 1990).

Throughout the Early Devonian the Malvinokaffric realm degenerated until final termination in the Givetian, though it maintained an endemic fauna until the Famennian (Boucot, 1985; Hallam, 1994; Meyerhoff et al., 1996; Blodgett and Stanley, 2008). Due to an abrupt Early Devonian global warming event the geographical distribution of the Malvinokaffric realm was reduced (Oliver, 1990; Boucot et al., 1969; Boucot, 1988). This extinction event reduced shelled fauna genera from 65 to 8 within the Parana Basin (Bosetti et al., 2011). The Malvinokaffric trilobites became extinct in the late Givetian coincident with the abrupt dispersal of warm-water taxa (House 1978; Leanza 1968; Boucot and Theron, 2001; de Melo, 1988; Aboussalam and Becker, 2011). Strong warming pulse in the late Givetian led to a lowering of the latitudinal temperature gradient, compounded by eustatic fluctuations, resulted in the restriction of the Malvinokaffric which continued throughout the Taghanic event (Aboussalam and Becker, 2011).

Evidence from the brachiopods *Australocoelia* and *Pleurothyrella*, *Tanerhynchia* distributions suggests South Eastern Australia (Tasmania and Victoria) and New Zealand were proximal to the Malvinokaffric realm's boundary with the Old World realm (Boucot et al., 1969).

#### Old World realm

Old World province Boucot et al., 1969 Old World realm Boucot and Gray, 1979 Old World realm Bigey, 1985

**Stratigraphic range:** Earliest Devonian to Carboniferous (Blodgett et al., 1990).

**Type:** Prague Basin (Chlupac, 1975) Bohemian Massif; Czech Republic.

**Diagnosis:** Equatorial realm with the highest levels of diversity and warm-water features such as carbonates, shallow subtidal fauna, reef or bioherm and evaporites (Chlupac, 1975; Blodgett et al., 1990; Hallam, 1994; Cocks and McKerrow, 1973). The Old World realm was derived from the Silurian 'North Silurian realm' (Boucot, 1974) and had significant Silurian holdovers such as eospirifers, orthids, atrypids, athyridids (Boucot et al., 1969; Boucot, 1985; Hallam, 1994). Eurasia was characterised by the trilobites *Acaste*, *Asteropyge*, *Neometacanthus*, *Treveropyge* and other asteropygids and *Homalonotus* with the trilobites traceable through South Asia and into Chitral, Pakistan (Kobayashi and Hamada, 1975).

Observed across western and arctic North America, Eurasia, North Africa, Australia, annexing part of the Eastern Americas and Malvinokaffric realms throughout the Middle to Late Devonian as extinction event compounded increasing global cosmopolitanism (Hallam, 1994; Boucot, 1985; Bambach, 2006). **Remarks:** First identified by Boucot et al., (1969), the Old World realm is divided into the Rhenish-Bohemian, Uralian, Cordilleran, Tasman, Mardoowarra, Eastern Australasia and New Zealand regions.

Since the classification of Boucot et al., (1969) multiple authors have reiterated the realm (Oliver, 1977; Bigey, 1985; Wang et al. 1984; Lieberman and Eldredge, 1996; Blodgett et al. 2001; Bosseti et al., 2011; Aboussalam and Becker, 2011 amongst others). The Old World saw Early Devonian provincialism steadily increase until it reached its maximum within the Emsian, with some fauna, such as rugose corals, presenting 91% endemism in some areas (Oliver, 1976). The transcontinental arch, which separated Devonian seas in the eastern and western North America, was an effective barrier to exchange between the Eastern Americas and the Old World realms, the cycles of transgression and regression resulting in local submergence and potentially contributing to the decrease in provincialism due to exchange and competition (Oliver, 1976; Rode and Lieberman, 2005). Old World realm genera, for example, have been located within the Michigan Basin and Hudson Bay lowland which led to the conclusion that a viable marine connection to the Old World existed (Kobayashi and Hamada, 1975; Van Der Voo 1988; Blodgett et al., 2002). Oliver (1976) notes that Old World fauna had dispersed to the Eastern Americas in greater numbers and with greater success.

The high rates of endemism in the Early and Middle Devonian waned into the Late Devonian (Young, 1981; Young et al., 2010). Zhao and Zhu (2010) proposed three Asian dispersal routes connecting Laurentia and Gondwana: the overlap of the northern, southern and circum-pacific ocean routes. These dispersal routes allowed shared brachiopod fauna between the Chinese terranes and Europe, North America, Siberia and Gondwana (Chen, 2004). Vertebrate fauna indicates similar patterns with Iran, Afghanistan, Azerbaidjan, Saudi Arabia, Turkey, Bohemia, France, Spain, Portugal, Bolivia, Venezuela, Colombia, Morocco, Libya, Algeria and South Africa presenting specific resemblance to Chinese species (Zhao and Zhu, 2010).

#### Cordilleran region

Cordilleran subprovince Boucot et al., 1969 Uralian-Cordilleran region Boucot, 1974 Cordilleran region Blodgett et al., 1990

# **Stratigraphic range:** Devonian (DeSantis and Brett, 2011). **Type:** Road River Group, Alberta.

Diagnosis: Warm-water western North American brachiopod fauna including Variatrypa arctica, Pentamerella, Spinatrypa and Warrenella (Warrenella) maia and the rugose coral Guerichiphyllum (DeSantis and Brett, 2011). The Eifelian Stony Hollow Event resulted in the disappearance of Variatrypa from Eastern Laurentia, the fauna persisting within the Cordilleran region (DeSantis and Brett, 2011). Western and Arctic North America (Nevada, southern California, British Colombia, Alberta, Manitoba, Yukon Territory, Northwest Territories and the Canadian Arctic Archipelago. Remarks: The Cordilleran region was situated within subtropical equatorial regions, distributed throughout interior and southeastern Alaska, Canada and western America (Morrow and Geldsetzer 1988; DeSantis and Brett, 2011; Wang et al., 2011). The region presents great diversity, including shell ornamentation potentially due to the migration and association with the Eastern Americas realm, particularly Appalachian brachiopods, gastropods, corals (DeSantis and Brett, 2011). Warmwater incursions from the Cordilleran region during the Kačák Event were observed from within the Appalachian, Michigan and Iowa basins and to a lesser extent the Wabash Platform area (Ohio and southeast Indiana (DeSantis and Brett 2011). Indicative of the Stony Hollow Event (late Eifelian) was the sudden expansion of the Cordilleran taxa into North America.

In the Early Devonian the Nevadan subprovince was relegated to the Eastern Americas realm its affiliation shifting in the Emsian, becoming distinctly Old World during the Eifelian (DeSantis and Brett, 2011). Originally based upon evidence from rugose corals and brachiopods, Pedder and Murphy (2004) argued that Rugosa no longer supported the Pragian brachiopod evidence that the Nevada platform biofacies were a western extension of the Eastern Americas realm into the Cordilleran province (Pedder and Murphy, 2004).

**Subprovinces included:** Cordilleran subprovince a subset of the Great Basin (Boucot et al., 1969; Kobayashi and Hamada, 1975). Alaska-Yukon subprovince (Blodgett et al., 1990, see Alaska-Yukon province). Nevada subprovince (Blodgett et al., 1990).

#### Alaska-Yukon province

Alaska-Yukon subprovince Boucot, 1974 Alaska-Yukon subprovince Blodgett et al., 1990 Alaska-Yukon province Pedder and Murphy, 2004

**Stratigraphic range:** Eifelian (Blodgett et al., 1990). **Type:** Nixon Fork terrane, Canada.

**Diagnosis:** Gastropods related to coeval forms in northwestern Canada. Interior and southeastern Alaska, the subprovince covers the Nixon Fork Terrane and Livengood terrane (Blodgett et al., 1990).

**Remarks:** The area distributed across the Nixon Fork and Livengood terranes, which is poorly constrained within the biogeographical hierarchy (Boucot, 1974; *contra* Blodgett et al., 1990). Limited to southeastern Alaska, its contemporaneous Early Devonian relationships tend towards northwestern Canada, suggesting a displacement of Alaska's 'suspect terranes'. The subprovince was an equatorial area that remained separated from the Great Basin of the Nevada province based upon rugose coral data (Blodgett et al. 2001; Pedder and Murphy, 2004).

#### Euramerican province

Euramerica (Cephalaspid) province Young, 1981. Euramerica province Afanasieva and Amon, 2013.

#### Stratigraphic range: Devonian.

Type: Timan-Pechora basin

**Diagnosis:** Defined by traquairaspids, pteraspids and cyathaspids across North America, the Canadian arctic and

Greenland (Young, 1981). The unit has radiolarian associations within marginal seas and shallow shelf epiplatforms.

**Remarks:** The province spans the entirety of the Devonian and is characterised by shallow shelf epiplatform and marginal sea environments (Afanasieva and Amon, 2013). This province, due to its large spatio-temporal distribution falls within both the Cordilleran and Ural regions of Boucot (1974). The region is assigned here to the Cordilleran region due to its prominence within western North America. Breakdown of subprovinces hypothesised due to the convergence of Baltica (Europe west of the Urals) with Laurentia and the consequent end of geographical barriers (Young, 1981).

**Subprovinces included:** European subprovince, North American subprovince, Northern subprovince (Afanasieva and Amon, 2013).

# Western Canada province

Western Canada province Boucot and Blodgett, 2001

#### Stratigraphic range: Early Devonian

**Type:** Hare Indian and Ramparts formations, Mackenzie Mountains, Canada.

**Diagnosis:** Gastropod fauna including *Tropidodiscus*, *Boiotremus*, *Bellerophon*, *Kodymites*, *new genus liospirinid*, *Stenoloron*, *Australonema*, *Platyceras*, *Orthonychia*, *Oriostoma*, *Semitubina*, *Murchisonia*, *Planitrochus* and *Perneritrochus* (Blodgett et al. 2001). Miogeoclinal shelf areas of British Colombia, southwestern Northwest Territories and the triangular, non-accreted portion of east-central Alaska.

**Remarks:** The Early Devonian brachiopod faunas of the Western Canada province were almost entirely distinguished from those in adjacent Alaska, which later accreted to the margin (Blodgett et al. 2001). While both Western Canadian and Alaskan accreted terranes were Old World, the fauna of the Western Canada province bore Uralian affinity.

## Nevada province

Nevada province Boucot, 1974 Great Basin province Pedder and Murphy, 2004

# Stratigraphic range: Early Devonian.

**Type:** Colis Creek member, McColley Canyon Formation, northern Roberts Mountains, eastern central Nevada.

**Diagnosis:** The Great Basin west of the transcontinental arch. Depauperate brachiopod fauna. In the early Pragian the province exhibited a low diversity fauna. The province began to decline in the late Emsian with the disappearance of Breviphyllidae and Papiliophyllidae was finally terminated with the early Eifelian arrival of the Old Word realm Cystiphyllidae, Ptenophyllidae and Stringophyllidae (Pedder and Murphy, 2004). **Remarks:** The Nevadan province was annexed by the Eastern America realm at the start of the Eifelian (Boucot, 1974). The Nevada province was primarily distinguished by the fauna of the Great Basin (Boucot, 1974) and despite being in close proximity to the Mackenzie and Appohimchi provinces each were distinct in the Pragian and Emsian (Pedder and Murphy, 2004).

# Mackenzie province

Mackenzie province Pedder and Oliver, 1990

Stratigraphic range: Pragian to Eifelian.

Type: Bartine Member, western central Nevada.

**Diagnosis:** Prominent coral fauna including Mucophyllidae, Spongonariidae, or Ptenophyllidae with the sole representative of Papiliophyllidae. Nevada, bound by the allochthonous Alexander and Farewell terranes of Alaska and British Colombia (Pedder and Oliver, 1990).

**Remarks:** The province is defined in the middle Pragian by 28 genera of which 27 are absent from Great Basin and all are absent from Appohimchi province. The strict generic differentiation within corals was used by Pedder and Murphy (2004) to further define previous provinces established by brachiopods (Boucot, 1974) and gastropods (Blodgett et al. 2001).

Eastern Australasia region regio nova

Etymology: Designation based upon largest area.

# Stratigraphic range: Late Devonian.

Type: MacDonnell Ranges, Amadeus Basin, Central Australia. **Diagnosis:** Freshwater and brackish assemblages, including tetrapodomorpha, the antiarch *Bothriolepis*, osteolepiform *Marsdenichthys longioccipitus* (Long, 1986) and the placoderm *Placolepis*, which is endemic to Eastern Gondwana, observed between North Eastern Queensland, central western NSW and the Transantarctic Mountains, Antartica (Johanson and Young, 1999; Young, 2005; Holland, 2010). Gastropod fauna include abundant bellerophontids in the Canning Basin, genera including Aglaoglypta, Plagiothyra, Pseudomphalotrochus indicating North American and European affinities (Cook, 2001).

**Remarks:** Eastern Gondwanan reefs collapsed in the Late Devonian ending the Tasman region (Webb, 1988). Some vertebrate taxa, such as *Bothriolepis*, survived into the Late Devonian (Johanson, 1998) when a more broadly dispersed vertebrate fauna typified Eastern Australasia. There is evidence of connection between the Eastern Australasia, Mardoowarra and Rhenish-Bohemian regions (Webb, 1988).

# New Zealand region

New Zealand subprovince Boucot et al. 1969

New Zealand region Boucot and Gray, 1979 New Zealand region Bigey, 1985

# Stratigraphic range: Early Devonian.

Type: Reefton group, New Zealand (South Island).

Diagnosis: A mixture of Tasman (Maoristrophia and Reeftonia), Malvinokaffric (Pleurothyrella and Tanerhynchia) and endemic (Allanetes and Reeftonella) brachiopod elements (Boucot et al., 1969). Found only within the Reefton Group and Baton Formation, West Coast, South Island, New Zealand (Boucot et al., 1969). Units termination is based upon the temporal range of definitive taxa, such as *Pleurothvrella venusta*. Remarks: The Devonian deposits within New Zealand are depauperate resulting in insufficient data to discern trends of Early Devonian (Bradshaw, 1999; R.A. Cooper pers. comm. 2016). Devonian New Zealand bares the hallmarks of shelf and shallow-water deposition, with reefs, stromatoporoids and bioherms observed and, in some formations, within an alternating sequence of thicker shelf mudstone (Fagerstrom and Bradshaw, 2002). The base of the Baton formation marks an abrupt increase in water depth with a change from arenaceous shelf sedimentation to deeper water, fine-grained lithologies (Bradshaw, 2000). The Baton fauna, from the Baton River series of seven members have been described as having Bohemian affinity, secondary to the Tasman region from which it split in the Early Devonian (Allan 1947; Plusquellec, 2015; Dowding and Ebach, 2016). It is possible that the New Zealand region is nested within that of the Tasman as both subprovinces within New Zealand (Baton and Reefton) exhibit strong relationships to the Melbourne zone of Australia's southeast (Dowding and Ebach, 2016). For instance, the unit is described as a transitional area between realms (the Malvinokaffric and Tasman region of the Old World, Shirley, 1938, Boucot et al., 1963), but its delineation is based upon a relatively depauperate fauna (Boucot et al., 1969; Boucot 1974). The Reefton Group falls within the Buller terrane and consists of 10 formations and five inliers of Emsian/Early-Middle Devonian age, the majority of which have been cited as presenting strong resemblance and shared association to Australia (Fagerstrom and Bradshaw, 2002; Wright, 1990; Pedder et al., 1970; Scott, 2013).

**Subprovinces included:** Reefton (Buller) subprovince (Dowding and Ebach, 2016).

# Rhenish-Bohemian region

Rhenish-Bohemian subprovince Boucot et al., 1969 Rhenish-Bohemian region Boucot 1974

**Stratigraphic range:** Early Devonian to Frasnian (Meyerhoff et al., 1996 **Type:** Prague Basin, Czech Republic.

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**Diagnosis:** Characterised by warm-water brachiopods *Athyris*, *Tropidoleptus*, *Pustulatia*, *Trematospira*, *Protoleptostrophia* and meristellids and the trilobite *Greenops* (Boucot, 1974).

**Distribution:** Europe from the western margins of the Russian platform, West and North Africa from Guinea north, Arabia and coastal Acadian parts of eastern North America including the Annapolis Valley of Nova Scotia, plus the coastal Maine and New Brunswick. Armorican Massif is notable for having Eastern American affinities within the Emsian (Boucot and Blodgett, 2001). The region shared a border with the Appohimchi subprovince (Boucot, 1974) and a boundary with the Eastern Americas realm near the St. Lawrence River in southwestern Nova Scotia from New Brunswick to Northeastern Mexico.

**Remarks:** Though initially identified by brachiopods, the Rhenish-Bohemian province has been subsequently identified using gastropods, rugose, corals, trilobites (Oliver and Pedder, 1989; Boucot, 1974). This warm-water region was derived from the Silurian Uralian-Cordilleran region and European province and had low energy reef environments with black shale facies surrounded by pelagic communities (Boucot, 1974).

**Subprovinces included:** Subprovinces do exist for this region, but are unrelated to those of Boucot. See Afanasieva and Amon, 2013

#### North Africa province

North African province Oliver, 1977

# Stratigraphic range: Early to Late Devonian.

Type: Rich Formation, Morocco.

**Diagnosis:** Characterised by braided fluvial and arch-basin systems upon the passive Gondwanan margin and a significant Silurian holdover (Carr, 2002; Lamotte et al. 2013). Distributed across North Africa, bound to the east and south by terrestrial environments and the Malvinokaffric (Boucot, 1974, 1988; Oliver, 1977,).

**Remarks:** The Silurian holdover present within the province included Bohemian elements that lasted throughout the Givetian (Boucot, 1988). The province became more cosmopolitan during the late Early Devonian correlated with the tectonic action of the Variscan (Hercynian) orogeny (Oliver, 1976; Carr, 2002; Lamotte et al. 2013). In association with the convergence of the Euramerican and Gondwanan continents, Eastern Americas realm rugose corals appeared within Africa, migrating either through breaks in the peninsula or through its southern edge (Oliver, 1976).

# Tasman region

Tasman subprovince Boucot et al. 1969

Tasman region Cocks and McKerrow, 1973 Tasman region Plusquellec, 2015

Range: Lochkovian to Frasnian.

Type: Garra Formation, Australia.

**Diagnosis:** Equatorial fauna of four brachiopod communities, generally within turbulent benthic level bottom communities (Boucot, 1974). Australia and New Zealand (Baton subprovince; Dowding and Ebach, 2016). Expands in the Middle Devonian to include New Zealand and eastern Antarctica.

**Remarks:** The region was distributed across eastern Australia from northern Queensland with the addition of New Zealand's northwestern Nelson (Boucot and Blodgett 2001). The region was geologically active with the eastern Gondwanan margin convergent within a back-arc setting and alternative extensional and contraction phases (Von Raumer et al., 2002; Fergusson, 2010; Boger, 2011). Following along the continental margin, the region encompasses myriad facies including low and high energy substrates, volcaniclastics, shallow marine and patch reefs complete with reef mounds and some megaturbidites forming within the forearc basin, freshwater, brackish, estuarine and fluvial deposition (Bradshaw, 2000; Talent et al., 2000; Fagerstrom and Bradshaw, 2002). Environmental variation facilitated the identification of multiple provinces and subprovinces within the region.

East Australia province

Wuttagoonaspid-Phyllolepid province Young, 1981

# Stratigraphic range: Emsian to Eifelian.

Type: Mulga Downs Group, western New South Wales. Diagnosis: Based upon the presence of the placoderm, *Wuttagoonaspis* in association with some crossopterygii, acanthodians and thelodonts (Young, 1981). Distributed across central Australia (Young, 1981; Neef and Larsen, 2003). **Remarks:** East Australia province has significant terrestrial and freshwater influence. The province was terminated with the Tasman region by the end of the Middle Devonian and was succeeded by the Eastern Australasia region.

#### Mardoowarra region nova regio

**Etymology:** Nyikina First Peoples for The Fitzroy River, Kimberly region within which the Canning Basin is located. **Stratigraphic range:** Early to Late Devonian.

**Type:** Virgin Hill Formation, Canning Basin, North Western Australia.

**Diagnosis:** Characterised by warm-water trilobite and ammonite assemblages (McNamara and Feist, 2008, McNamara et al., 2009). Endemic taxa include *Gondwanapis spinosa* and *Globoharpes*; the presence of *Eskoharpes* indicating a strong Rhenish-Bohemian influence (McNamara et al., 2009). The region is distributed across north western Australasia through to Antarctica and India in shelf and reef to pelagic environments. **Remarks:** The region shows considerable faunal exchange with the Old World, ammonite fauna such as *Manticoceras* found also in Euramerican and the Ural region (Day, 1988; McNamara et al., 2009). The presence of the brachiopod *Tenticospirifer columnaris* in northwestern Australia (Roberts et al., 1972) is indicative of a biogeographic relationship with Western Laurussia (Ma and Day, 2000). The region terminates in the Late Devonian and is annexed by the Western Gondwana realm.

# South China region

South China province Young, 1981 South China region Boucot and Gray, 1979 South China region Boucot and Blogett, 2001

# Stratigraphic range: Devonian.

**Type:** Hexian Formation, Guangxi Zhuang Autonomous Region, China.

**Diagnosis:** Highly endemic in the Early Devonian, the equatorial unit has a strong freshwater influence and is characterised by galeaspid and polybranchiaspid agnathans and placoderms yunnanolepid antiarch and quasipetalichthyids (Young, 1981; Young et al., 2010). The unit included China south of the Tsin Ling Fold Belt (Young, 1981), northern Vietnam, Western Kunlun, Tarim and the Pan-Cathaysian area (Boucot and Blodgett 2001; Chen, 2004; Zhao and Zhu, 2010). The region, despite increasing external influence, maintained a strong endemic element until the end of the Devonian (Young, 2006, Young et al., 2010 and Zhao and Zhu, 2010).

Remarks: The associations of the south China region have come under much scrutiny, in part, due to the controversies surrounding its Devonian location (Oliver, 1977; Young et al., 2010). The documented relationships of the South China region include the Urals, Russian Platform, North China, Australia and Saudi Arabia (Boucot and Blodgett, 2001; Zhao and Zhu, 2010; Chen, 2004; Young et al., 2010). The relationship with Australia has proven of specific interest due to the potential for the South China region and associated blocks to act as a 'stepping stone' between Gondwana and Laurussia via Kazakhstan during the Givetian through to the Late Devonian (Li et al., 1993; Young, 2006, Zhao and Zhu, 2010). Increasing faunal exchange with Asia during the Devonian may have been initiated with Pragian-Emsian faunal turnovers in the South Chinese assemblages, with the Tarim Block withdrawing throughout the Late Devonian and into the Carboniferous (Young and Janvier, 1999; Young et al., 2010; Chen, 2004). The 'stepping stone' model presents itself as an alternative to distance dispersal between the Chinese blocks or the proposed Early/Middle Devonian closure of the ocean

between Western Gondwana and Laurussia (Young, 2006) though the theory is unsupported by Blieck et al., (2002).

Young et al., (2010) used the regions biogeography to comment on the area's geological relationships, stating that the hypothesis of Metcalfe (1996) and Zhao et al., (1996) that the China blocks and associated terranes originated from the Northern Gondwanan margin were contradicted by the placoderm data.

# Junggar-Xinan province

Junggar-Xinan province Hou, 1981

### Stratigraphic range: Devonian.

Type: Mongkelu Formation, Xinjiang, China.

**Diagnosis:** Abundant benthos, scarce nektonic organisms within a platform setting, with European and North American brachiopod affinities (Hou, 1981). Geosynclinal setting with volcanics and clastics. Characteristic taxa include the brachiopods Leptostrophia, Rhytistrophia, Gladistrophia, Megastrophia, Leptaenopyxis amongst others in three assemblages (see Hou 1981). The unit lies between the Sino-Korean and Tungrian landmasses, including eastern and western Junggar in Xinjiang, the Northern Tianshan Mountains, Inner Mongolia, northern northeast China, the Beishan Mountains, east to the Okhotsk Sea, west to the Balkash Lake (Hou, 1981). **Remarks:** The brachiopod assemblages make the province unique intermediate between the Old Word and Eastern Americas realms. Middle Devonian brachiopods relatively unknown, represented by Early Devonian holdovers. Some Middle Devonian correlation with the North American Hamilton and Onondaga formation; Appalachian province affinities shown through mutual absence of Old Word stringocephalids.

#### South China province

South China province Hou, 1981 Galeaspid-yunnanolepid Young, 1981

#### Stratigraphic range: Devonian.

**Type:** Putonggou Formation in the Diebu area, West Qinling, China.

**Diagnosis:** The benthic platform fauna were highly endemic including the brachiopods *Orientospirifer*, *Aeptalium* and *Kwangsirhynchia*. The *Karpinskia-Spirigerina* assemblage bore Ural and European influence. Platform sediments. The unit was distributed across southern regions of China, the eastern extension of the Ural-Tianshan Marine belt and the South Tianshan Mountains (Hou, 1981). The vertebrate assemblage was defined by the presence of the endemic galaespid and polybranchiaspid agnathans in association with gnathostome placoderms yunnanlepid antiarchs and quastipetalichthyids to the exclusion of holonematids and coccosteids characteristic of China in other regions (Young, 1981). Continental South China type is based upon galeapsid distribution (Zhu, 2000). **Remarks:** South China and Junggar-Xinan provinces separated by the Tarim and Sino-Korean landmasses. The province underwent Early Devonian tectonic events resulting in increased provincialism. During the Late Devonian cosmopolitan fauna appeared in the province in particular the brachiopod *Eoperegrinella baschkirica*, a genus identified in Poland, North America, North Africa and the Urals (Huo, 1981).

South China, during the Devonian, was located north of the palaeoequator. This province presents an highly endemic vertebrate fauna with the migration of cosmopolitan taxa observed within the region by Middle Devonian time, though the province retained its endemic characters into the Late Devonian.

**Subprovinces included:** South Tianshan, Southwestern and South subprovinces (Hou, 1981).

# Uralian Region

Uralian subprovince Boucot et al., 1969 Uralian region Boucot, 1974

#### Stratigraphic range: Devonian.

**Type:** Pai Hoi and Vaigatsch in the Urals and the Solovien limestone, Altai Mountains.

**Diagnosis:** Characteristic brachiopod forms include *Sibirihynchia, Janius, Karpinskia, Ivdelina* and endemic uncinuloids and gypiguloids. Abundance of brachiopods distinguishes this region from the Cordilleran, which is comparatively depauperate (Boucot et al., 1969). Brackish to nonmarine deposition. The unit includes the east and west Urals, Siberia including Taimyr, Kolyma, Chukotka, Kuznetsks Basin. Tien Shan, southeastern Kazakhstan, plus the Farewell, Alexander and Arcto Alaska Terranes.

**Remarks:** The region was descendent from the Silurian Uralian-Cordilleran region (Boucot, 1974).

# Balkash-Mongolo-Okhotsk province

Balkash-Mongolia-Okhotsk region Hou and Boucot, 1990 Balkash-Mongolo-Okhotsk province Boucot and Blodgett, 2001

Junggar-Mongolo-Okhotsk region Wang et al., 2013

# Stratigraphic range: Early Devonian.

Type: Great Khingan Range, China.

**Diagnosis:** Characterised by the brachiopod fauna *Acrospirifer, Areostrophia, Aulacella, Brachyspirifer, Coelospira, Dalejina, Megastrophia, Paraspirifer* and *Protochonetes* (Wang et al., 2013). Endemic fauna punctuated by Tasman and Eastern American elements (Boucot and Blodgett, 2001). The unit is inclusive of Lake Balkhash of

southeastern Kazakhstan, Mongolia, Neimonggol and the Greater Khingan Mountains in Heilongjiang (Boucot and Blodgett, 2001; Wang et al. 2013).

**Remarks:** The history and provinces of this region are confused somewhat by inconsistency of area nomenclature. Competing interpretations by Hamada (1971), Hou (1981), Hou and Boucot (1990) and Boucot and Blodgett (2001) are resolved within Wang et al., (2013). Wang et al., (2013) assigned the Altai-Sayan and Junggar-Balkhash provinces of Hamada (1971) (now subprovinces) to the Balkash-Mongolo-Okhotsk region, arguing towards joining Balkash-Mongolo-Okhotsk and Junggar-Mongolo-Okhotsk as a single province. To solve these inconsistencies the Balkash-Mongolo-Okhotsk is reassigned to province within the Uralian Region, consistent with the characterisation of Lindsey-Griffin et al., 2008 **Subprovinces included:** Balkash-Mongolo-Okhotsk subprovince, Junggar-Balkash subprovince (Hamada, 1971),

Altai-Sayan subprovince (Hou and Boucot, 1990).

#### Siberian province

Amphiaspid (Siberia) province Young, 1981 Siberian region Lebedev and Zakharenko, 2010 Siberia province Afanasieva and Amon, 2013

# Stratigraphic range: Early Devonian to middle Frasnian.

**Type:** Timan-Pechora basins, Timan Range and the Ural Mountains in northern Russia. For vertebrate fauna, the Bel'kovsky-Nerpalakh trough, Russia (Kos'ko and Korago, 2009).

**Diagnosis:** Young (1981) characterised the province by amphiaspid heterostracans and *Gerronaspis*, in association with acanthodians, porolepid rhipidistians, palaeoniscoids and placoderms. The area is spread across the Siberian platform, and gulf with potential salinity barriers inclusive. The diagnosis of Afanasieva and Amon (2013) is based upon endemic radiolarians. Typically, clayey carbonate strata with relatively depauperate marine fossils.

**Remarks:** A marine transgression initiated in the late Middle Devonian reached a maximum in the Frasnian reducing the size of the continental assemblages, with Givetian fauna poorly known (Lebedev and Zakharenk, 2010). The endemic osteostracan *Ilemoraspis* characterises the area's vertebrate fauna (Lebedev and Zakharenk, 2010). The heterostraci are represented by *Putoranapsis* and *Aphatapsis* (*Halstead*, 1973).

Transport between the three main Chinese blocks (Tarim, South China and North China), Siberia and Euramerica was present in the Early Devonian, facilitated by the southern Circum-Panthalassic ocean route or the northern route through Kazakhstan (Young 2005; Zhao and Zhu, 2010), though this theory is unsupported by Blieck et al. (2002). Lower Devonian biogeographic links based on brachiopods, suggest that the southwest Alaskan Farewell terrane represented a rifted continental margin sequence from the Siberian continent (Blodgett et al., 2002).

Though the province maintained an endemic element throughout the Late Devonian, the radiolarian assemblages in particular reflect increased migration from Euramerican, Ural and Australian provinces (Blodgett and Boucot 1999; Boucot and Blodgett, 2001; Afansieva and Amon, 2013). The Amphiaspid province of Young (1981) was, however, limited to the region west of the Tuvan Massif. The area was characterised by platforms seagulfs of varying salinity, with infrequent, clayey carbonate strata. The province provides evidence of significant Middle Devonian migration from the Australian province.

**Subprovinces included:** Rudny Altai subprovince, Western Siberia subprovince (Afanasieva and Amon, 2013).

#### Ural-southern Tianshan province

Ural-southern Tianshan province Hamada, 1971 Ural-southern Tianshan province Huo and Boucot, 1990 Ural-southern Tianshan province Wang et al., 2013

# Stratigraphic range: Devonian.

Type: Gorny Altai, Siberia.

**Diagnosis:** Characteristic fauna includes the brachiopods *Glossinulus (Glossinotoechia), Karpinskia* and *Nikiforovaena* (Wang et al., 2013). Distributed across Central Asia from Chelyabinsk to Khabarovsk and Northern Mongolia (Wang et al., 2013). Serov, Belaja River, Kuznetsk Basin, Gorny Altai, Mongolian Altia and Tarim.

**Remarks:** In the Early Devonian, the western margin of the Kazakhstan plate, eastern Siberian plate and northern Eastern European plate formed the Ural-Tianshan Ocean and tectonic region. The area presents strong Ural affinities, especially within the Altai-Sayan subprovince (Wang et al., 2013). Significantly, the province also showcases many Balkhash-Mongolo-Okhotsk elements, this is potentially due to the analogous tectonic events within the areas. The relationship was maintained throughout the Late Devonian during the processes of accretion and collision along the Hercynian fold belt and the Ob-Zaisan folded system (Dobretsov and Kirkdysahkin, 1994; Wang et al., 2013). Area possibly subsumed as a subprovince of the South China province (Hou, 1981).

#### Tuva province

Tannuaspid (Tuva) province Young, 1981

#### Stratigraphic range: Early Devonian.

**Type:** Chondergeyskaya, Samagaltayskaya and Kendeyskaya Group of the Tuvin depression in southwestern Tuva (Afanasieva and Janvier, 1985). **Diagnosis:** Endemic Siluro-Devonian ostracoderms including osteostracan *Tannuaspis* and *Tuvaspis*. Distributed across the Tuvan Massif, Tuva-Minusinsk-Kusnetsk region.

**Remarks:** The Tunnaspid province extends though the Tuva-Minusinsk-Kusnetsk region located on the eastern side of the Siberian continent (Young, 1981). The province had some faunal exchange with the Euramerican province (Young, 1981).

# Western Gondwana realm nova regio

Etymology: Designation based upon largest area.

Stratigraphic range: Late Devonian.

Type: Parnaiba Basin, Brazil.

**Diagnosis:** Cold-water, Appalachia, South America, South Africa and Antarctica south of Victoria Land. Depositional trend that is strongly controlled by fluvial input into a shallow marine environment (Ponciano and Della Favera, 2009) bearing gastropods (*Bucanella dereimsi*), trilobites (*Burmeisteria*, *Rhenops*), bivalves (*Modiomorpha* cf. *M. concentrica*, *Nuculites* cf. *N. africanus*), brachiopods (*Notiochonetes* sp., *Pleurochonetes Pustulatia* sp., *Schuchertella* sp.) and *Spongiophyton* (Wood, 1995; Lieberman and Kloc, 1997; Ponciano and Della Favera, 2009; Leme et al., 2013).

**Remarks:** The realm had mixed Eastern Americas realm and Malvinokaffric realm influences with significant holdovers from the annexed realms (Wood, 1995). The aforementioned realms suffered a collapse of their shelly fauna, the general basis for their characterisation (Boucot et al., 1969), in the late Middle Devonian (Bosetti et al., 2011). Antiarch fauna maintained their presence within the region throughout the Late Devonian (Wood, 1995).

# **Extinction events**

Zlihov event (early Emsian)

**Distribution:** Europe, associated with an early Emsian, transgressive event recognised in Australia, Siberia and Prague basin (Talent and Yolkin, 1987; House and Kerr, 1989; Grahn and Paris, 2011).

**Diagnosis:** The Zlihov event is characterised by the loss of the mimosphinctid and auguritid ammonoids (House and Kerr, 1989) and associated with high chitozoan abundance but low diversity (Grahn and Paris, 2011).

**Discussion:** The Zlihov event is associated with gradual oceanic deepening and deposition of black, calcareous shale facies with a subsequent regression at the base of the Pragian (House and Kerr, 1989). The observation of pyritic preservation is indicative of anoxia with consequent suggestion of ocean overturning as a mechanism for the spread of anoxic waters across oceanic shelfs (House and Kerr, 1989).

Chotec event (early Eifelian)

**Distribution:** Czech Republic, Morocco, Eifel Hills, Rhenish Slate Mountains, Armorican Massif, Cantabrian Mountains, Eastern Iberian Chains, Portugal, Siberia, Ural and the Appalachian Basin (Vodrazkova et al., 2013).

**Diagnosis:** Trilobites, such as coarsely sculpted and large species of the phacopidae, became extinct during this interval (McKellar, 2006). Within the Hercynian facies, the deposition of the black shales is contemporaneous with the appearance of the ammonoid *Pinacites jugler*, and in the Rhenish the disappearance of the brachiopod *Alatiformia alatiformis* (Ernst et al., 2012).

**Discussion:** Linked and considered to overlap with the Taghanic event in Morocco, the event is associated with marine lowstand and shallow-water carbonate production followed by transgressive series and the deposition of black shales (McKellar, 2006). Oxygen consumption through the degradation of newly heightened nutrient availability is believed to have led to the extinction and/or migration of benthic taxa (Vodrazkova et al., 2013).

Daleje event (middle Emsian)

Distribution: Barrandian Basin, Prague Basin.

**Diagnosis:** Local extinctions, specifically the elimination of the dalmanitid trilobites eliminated from the Prague Basin in association with shale sedimentation (Budil et al., 2009).

**Discussion:** Associated with eustatic sea level rise and subsequent deposition of sharp rise in tetaculite-rich shales across the Old World Faunal realms, minor faunal impacts (House and Kerr, 1989). Within the Barrandian Basin, the Koneprusy reef complex was partially surfaced and eroded at the Zlichovian-Dalajan boundary (Suchý et al. 2012). Eustatic sea level rise, localised extinction (Old world realm; Prague Basin) (House and Kerr, 1989; Budil et al., 2009).

Middle Devonian biocrisis (late Eifelian-Givetian)

**Distribution:** Predominantly limited to the Laurussia (Old red continent). Depositions found in the Prague Basin, Germany, Southwest England, Scotland, Southern France and Northern Spain. Evidence outside of the Old Red Continent comes from Morocco, New York State Northern America, South China and, Australia (House, 1996; House and Kerr, 1989; DeSantis and Brett, 2011; Jurina and Raskatova, 2011).

**Diagnosis:** The Middle Devonian (late Eifelian) biocrisis is an interval that can be separated into three distinct events, being the Bakoven, Stony Hollow and ultimately the Kacak event in the *ensensis* conodont zone (DeSantis and Brett, 2011). Correlation between the Kacak member recognises the event within *hemiansatus* Zone, the upper *kockelianus* Zone and the overlying Roblin member, including regions in Scotland and

Estonia (Jurina and Raskatova, 2011; Mark-Kurik and Poldvere, 2012).

**Discussion:** The Bakoven event, named after the and found within the *Bakoven australis* to *eiflius* zones within the Appalachian Basin and contemporaneous northern America, is marked by a loss of species diversity, eustatic deepening and hypoxia (DeSantis and Brett 2011).

Stony Hollow event (*kockelianus–eifelis* zone) saw the incursion of tropical old world, Cordilleran province taxa into the sub-tropical to temperate shelf region of eastern North America (DeSantis and Brett, 2011). The primary signature of the Stony Hollow (late Eifelian) incursion was an abrupt expansion of OWR Cordilleran province taxa into eastern North America. The immigration records a major expansion of biogeographic boundaries, as most of the taxa, or closely-related forms, remained in the Old World realm Cordilleran region throughout and after the Stony Hollow interval (DeSantis and Brett, 2011).

The Kacak event is recognised in conodonts and dacryoconarids and ammonoids (House, 1996; DeSantis and Brett, 2011). Identified by hypoxic or anoxic shales and limestones coupled with eustatic sea level rise (House, 1996) has been estimated to have lasted between 200,000 and 700,000 years in various locations (House and Kerr, 1989; Ellwood et al., 2011). The Kacak event is associated with geochemical anomalies in nickel, carbon and oxygen isotopes and Total Organic Carbon (TOC) as well as changes in lithoferric constituents identified by excursions in magnetic susceptibility (House and Kerr, 1989; House, 1996). Large eustatic sea level rise and widespread anoxia produced a downturn in trilobite diversity including minor effects within the phacopids (McKellar, 2006).

# Taghanic (late Givetian)

**Distribution:** Hamilton Fauna Northern Appalachian Basin, North American Basin (Laurentia), Morocco, Moscow Russia, Ardennes, Rheinisches Schiefergebirge, Prague Basin, Morvarian Karst (McKellar, 2006; Baird and Brett, 2008).

**Diagnosis:** Regionally, clear carbonate deposition transitions to increasingly anoxic black muds and limestones with pelagic faunal incursions into sheltered basins (Baird 2008). The alteration of habitat, highstand and associated invasion lead to the major faunal fluctuations; notable extinctions include the *Sobolewia* (Sobolweiidae), with genera of ammonoids, goniatites, corals and brachiopods all substantially effected (House and Kerr, 1989).

**Discussion:** The Taghanic bioevent describes a ~ 500,000 year cumulative series consisting of four events equally split into the Lower Tully and Taghanic events that may have been as severe as the Frasnian-Famennian extinction (House and Kerr, 1989; Aboussalam and Becker, 2011; Baird and Brett, 2008; McKellar, 2006). The Taghanic bioevents were preceded by a 4–5-Ma interval of relative stability, both ecological and evolutionary, during the majority of the early and middle Givetian (Baird

and Brett, 2008). The Taghanic bioevent was set during the second and third collisional tectophases of the Acadian Orogeny (Baird, 2008; Zambito, 2011). Global increases an aridity, temperature were coupled with marine highstand, rapid eustatic sea level fluctuations decreased oxygenation of epicontinental seas and extreme marine highstand (Marshall et al., 2011).

Kellwasser crisis (late Frasnian)

**Distribution:** Related epicontinental and basinal facies have been identified in Gondwana, Siberia, South China and Laurussia (Carmichael et al., 2014), suggests global event (Waters et al., 2013).

**Diagnosis:** The Kellwasser extinction of 13–40% of all families and 50–60% of genera, with only minor vertebrate fauna loss (Sole and Newman, 2002; Sallan et al. 2010).

Discussion: It is limited by two bands of anoxic shale, which may in turn suggest two distinct extinction events, and was preceded by an extended period of biodiversity loss (Sole and Newman, 2002; Balter et al., 2008). Protracted nature of the Kellwasser event is supported by trilobite adaptive morphologies, small eyes and wide respiratory brims an adaptation to the high turbidity and low oxygenation associated with the event (Balter et al. 2008). Exclusively marine, shallow warm-water taxa, including vertebrates such as antiarchs, jawless fish and placoderms, suffered 65% extinction (Bambach, 2006; Sallan et al. 2010). The protracted nature and similarity of the Kellwasser and Hangenberg events often see some of the extinctions of the Kellwasser attributed to the later Hangenberg event, due to the poor Famennian fossil record (Algeo et al., 1998). The extinction is thought to have two pulses, the first regressive phase lasting 400 kyr and the second transgressive leasing 50 kyr (Chen and Tucker, 2003).

Hangenberg event (Famennian)

**Distribution:** Gondwana, Siberia, Laurussia, South China, indicative of a global event (Waters et al., 2013).

**Diagnosis:** Widespread anoxia in oceanic bottom waters, increased carbon deposition, and the continued reduction and depletion of shallow warm-water taxa and habitat (Algeo et al., 1998). Overall extinction peaked at 31% with stromatoporoids, rhynchonellid brachiopods, ammonoids, trilobites, placoderms and osteichthyes suffering rates of 70% (Bambach, 2006). The extinction of terrestrial taxa, up to 40% of vertebrates, have been set as a precursor to the Carboniferous Romer's gap (Sole and Newman, 2002; Ward et al., 2006; Sallan et al., 2010).

**Discussion:** The cause of the Hangenberg event remains contentious. Forest fires, soil erosion, glacial events and eutrophication have all been cited as potential causes of the Late Devonian extinction events (Algeo et al., 1998; Murphy et al. 2000; Racki et al., 2002; Tribovillard et al., 2004; Bambach, 2006; Kazmierczak et al., 2012; Kaiho et al., 2013; Carmichael et al., 2014), but discussions are focussed primarily upon transgressive and regressive cycles and, tectonic action (Sandberg et al., 1988; Joachimski and Buggisch, 1993; McGhee, 1991; Chen et al., 2002; Bond et al., 2004; Tribovillard et al., 2004; Bond and Wignall, 2008; Chen et al., 2013).

Causal links between the evolution of increased arborescence and seed habit and the extinction through the rapid decrease of atmospheric  $CO_2$  from 4000 ppm to nearly present-day values of about 350 ppm during the latest Devonian (Royer 2006 in Carmichael et al., 2014). These interactions between primary and secondary causes, such as tectonic movement, atmospheric eutrophication, could have coincided to bring about the Late Devonian extinctions (Algeo et al., 1998; Carmichael et al., 2014).

# Conclusions

The work of Boucot has formed a solid foundation for past and present Devonian bioregionalisations. This study has reviewed the global bioregionalisations under stringent conditions to provide a standardised diagnosis of Devonian biogeographical units within a formalised hierarchy. The establishment of three new areas provides the Devonian with its first complete bioregionalisation. Though both authors acknowledge the limitations and problematic description of a cosmopolitan Old World realm in the Late Devonian, no viable alternative has been offered under Boucot's framework. This review instead amended the failure to assign areas, completed the bioregionalisation and will now act as a hypothesis for any future empirical tests of Devonian bioregionalisation. Until then, this interim bioregionalisation and review will offer a template for future studies.

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# **Compliance with ethical standards**

**Conflict of interest:** The authors declare that they have no conflict of interest.

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