A field-based and literature-based study of the *lundgreni* (late Wenlock, Silurian) graptoloid extinction event

Lucy A. Muir

PhD thesis, University of Edinburgh, 2003

Abstract

The extinction event at the end of the *lundgreni* graptoloid biozone (Homerian, Wenlock, Silurian) was one of the most severe to affect graptoloids during the Silurian. There are many hypotheses of what caused the extinction, but little work has been done relating the extinction to graptoloid ecology. In this study, the event has been investigated in the field and using existing literature. Fieldwork was conducted in the UK and in Australia, with the aims of studying environmental changes at the time of the *lundgreni* event. Results from fieldwork do not support the hypothesis that the *lundgreni* event was caused by anoxia. Taxonomic descriptions of three monograptids and five retiolitids from Australia are also given.

Data gathered from the literature has been used to compile a global database of species occurrences before and after the event. A comprehensive review of the occurrence of Homerian graptoloids is also given. The global literature survey of pre- and post-extinction faunas revealed a much greater diversity immediately after the extinction than had previously been suspected. It appears that many species survived the extinction event in very small areas, and, if a species survived the extinction initially, it had a high chance of surviving thereafter.

Both the field-based and the literature-based studies have been used to test hypotheses of the ecological causes of the *lundgreni* extinction. The hypotheses considered include that extinction is random, that there is a correlation between geographical distribution and extinction probability, and that the life history strategy of a species (whether the species is K- or r-selected) affects extinction probability. At the family and sub-family level extinction is random. Numbers were too small to test at genus level. Extinction likelihood does not appear to be linked with geographical distribution for monograptids. However, for retiolitids, those species with restricted ranges were more likely to become extinct than those with wide ranges. The limited evidence available suggests that life history strategy is important in whether a species survived the extinction or not, with K-selected species being less likely to survive than r-selected ones.

"Shall I tell you something else?" said Rincewind, a little more calmly. "This world is an anvil. *Everything* here is between a rock and a hard place. Every single thing on it is the descendant of creatures that have survived everything the world could throw at them."

Pratchett *et al.* 1999, p.298.

Acknowledgements

I would like to thank my supervisors, Euan Clarkson, Barrie Rickards and Sue Rigby, for all their help and support over the last four years. I am also grateful to the members of the British and Irish Graptolite Group, for helpful discussions; the librarians of Edinburgh University (but not the cataloguing system), Cambridge University and the Natural History Museum, London, for access to obscure literature; and Mike Dorling (Sedgwick Museum), Bob Owens (Cardiff Museum) and Bob Jones (Australian Museum) for access to specimens in their care. Phil Crabb (Natural History Museum) photographed the graptolites in Chapter 4. Finally, thanks are due to my parents and Joe Botting, for things too numerous to mention.

This PhD was funded by NERC, grant number GT 04/99/ES/78.

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1. Introduction

Extinction has been highly significant in the history of life; to a good first approximation all species are extinct (over 99% of species are extinct, McKinney 1997). *Extinction events* occur on both large and small scales. Kaljo *et al.* (1996) defined a scale of extinction intensity, from first-order events such as the end-Ordovician mass extinction to fifth-order events, which involve diversity changes in one or two groups. Extinction events may be caused by either elevated extinction rates, or depressed origination rates, or a combination of the two. The question of what exactly constitutes an extinction event is discussed in Chapter 2.

There are two types of extinction: *pseudoextinction*, where one species evolves into another, and *true extinction*, where every member of a species dies without surviving progeny. The first type is an artefact of our classification system but is significant in that it masks the presence of the second type. However, pseudoextinction is a problem when trying to decide whether or not a particular extinction event is an extinction event or an artefact of the fossil record.

Some types of organisms are more likely to become extinct during extinction events than others. In general, large body size, low abundance and specialisation increase a species' likelihood of extinction (McKinney 2001). Studying extinction events in the past, and discovering why some types of organisms are more vulnerable to extinction than others, may help with conserving species affected by the current extinction event.

Graptoloids are ideal fossils for studying extinction events and recoveries because there is a reasonable number of species, their stratigraphic ranges are increasingly well known, an extremely detailed biostratigraphic scheme is available, they suffered many extinction events, and the number of specimens available is effectively unlimited (Rickards 1988).

Graptoloids suffered many extinction events during the Silurian: five in the Llandovery, three during the Wenlock, three more in the Ludlow and one during the Přídolí. They finally became extinct in the lower Devonian. All these events are discussed in Chapter 2.

One of the most severe extinction events (in terms of percentage extinction, termination of lineages and subsequent low diversity) occurred at the end of the *lundgreni* Zone (late Wenlock) (Melchin *et al.* 1998). The classic picture of the event is that *Cyrtograptus* and hooked monograptids (*Monograptus sensu stricto*), as well as other monograptids and many species of retiolitid, became extinct. After the extinction there was an interval of low diversity, with only the monograptids *Pristiograptus dubius, P. parvus* and the retiolitid *Gothograptus nassa* occurring. Rediversification of both monograptids and retiolitids occurred during the *praedeubeli-deubeli* and *ludensis* zones. However, there have been reports of *Cyrtograptus, Monograptus sensu stricto* and *Testograptus testis* surviving the extinction event in Australia (Rickards *et al.* 1995a), and there are other reports of *Monograptus s.s.* occurring after the extinction. This is discussed further in Chapters 2 and 4.

There are many hypotheses as to what caused the *lundgreni* event, which are discussed in detail in Chapter 2. The hypotheses advanced have been to do with physical causes, for example bolide impact (Berry *et al.* 1988), an increase in oceanic anoxia (Quinby-Hunt & Berry 1991) and a decrease in oceanic anoxia (Koren' 1987; Štorch 1995). However, none of these hypotheses address the question of how a physical change affects individual graptoloids and graptoloid communities such that every individual dies without surviving progeny. To answer this requires a knowledge of graptoloid ecology.

There is general consensus on some aspects of graptoloid ecology: they were animals; they were planktic (e.g. Bulman 1970 p.V91); they were filter feeders (e.g. Rigby & Fortey 1991) and they were at least to some extent depth stratified (e.g.

Berry & Boucot 1972a; Cooper *et al.* 1991). Other aspects of their ecology, for example whether or not they were automobile, are still matters for debate (e.g. Kirk 1978; Rickards 1975). They must have been able to at least change their depth in the water column (Rigby & Dilly 1993), but whether they did this passively by changing their buoyancy or actively by swimming is not known. To a good first approximation, all graptoloids had the same mode of life. At the moment we cannot say how the niches of different species may have differed. Looking at the range of morphologies present in graptoloids it is tempting to say that they must have done different things ecologically, but what things? Did graptoloids of different morphologies exploit different foodstuffs? Did different species have different reproductive strategies, such as semelparity (reproducing once) and iteroparity (reproducing many times)?

The main problem in trying to understand graptoloid ecology is that they are all extinct and no good modern analogue exists. Their living relatives, the pterobranchs *Rhabdopleura* and *Cephalodiscus* are all benthic and encrusting – a completely different mode of life. The only modern filter/suspension feeding colonial macrozooplankton are the urochordates (e.g. *Pyrosoma*). The Portuguese-man-o-war (*Velella*) is also colonial macrozooplankton, but is predatory rather than filter-feeding (Barnes *et al.* 1994), so is not such a good analogue.

How can we obtain a better understanding of graptoloid ecology? Some things, of course, will never be known, colour for example. However, our knowledge can be improved. Population analyses such as those of Rigby (1993) can show whether graptoloid colonies grew throughout their lives or reached a maximum size, and can show whether growth was continuous or seasonal. In addition, the life history strategy of a species (K-selected or r-selected) can be worked out using survivorship curves. (K-selected species are large, long-lived and tend to have few offspring, most of which survive; r-selected species are small, short-lived and tend to have many offspring, few of which survive.) This is discussed further in Chapter 6. Life history strategies are highly significant for such things as extinction vulnerability.

There are two ways of studying extinctions: field-based and literature-based studies. Both methods have advantages and disadvantages. The advantage of studying extinctions in the field is that the study can be very precise in time. The disadvantage is that obtaining a global overview using only this method would be the work of a lifetime. The advantage of a purely literature-based study is that it is easy to get a global overview. The disadvantages are that the worker may not be aware of taxonomic problems, for example synonymies or a single taxon having more than one name, and the temporal resolution is relatively coarse, because of the need to correlate between different areas, some of which will have more refined biostratigraphic schemes than others. This study has utilised a combined approach – studying the *lundgreni* extinction in detail at exposures in Wales and in Australia and compiling a global database from the literature. Data from both the field-based and the literature-based sections are used to test hypotheses of the ecological causes of the *lundgreni* extinction. Holland (1985) made the point that it is easier to manipulate data than to gather it. In this work I have attempted to do both.

The hypotheses that will be tested are:

1. Extinction is random – i.e. no species is more or less likely to go extinct than any other. This hypothesis is the null hypothesis when considering the causes of extinctions. If this is not the case, this suggests that some species have certain characteristics that give them a higher probability of extinction.
2. There is a correlation between geographical distribution and extinction probability. Theoretically, a taxon with a wide geographical range is more likely to survive an extinction event than a taxon with a narrow range, because in the wide range there is a greater chance of a refugium existing (Rosenzweig 1995 p.120).
3. There are latitudinal variations in extinction patterns.
4. K-selected species are more likely to go extinct than r-selected ones.
5. Rare species are more likely to go extinct than common species.

All these are discussed in detail in Chapter 6.

In Chapter 2, Silurian graptoloid extinction events are reviewed and common patterns identified. The *lundgreni* event is discussed in detail, especially hypotheses for the cause of the extinction. Field studies of the interval before and after the event in the UK and in Australia are presented in Chapters 3 and 4. Chapter 5 reviews the occurrence of species globally before and after the *lundgreni* event, and hypotheses as to why particular species went extinct are tested in Chapter 6. The findings of this study are discussed in detail in Chapter 7 and suggestions offered for further work.

2. Literature review

This chapter summarises previous research on graptoloid extinction events during the Silurian and discusses common patterns between these events. The *lundgreni* event is discussed in detail and the current state of knowledge summarised. Various hypotheses for the cause of the *lundgreni* extinction have been proposed; these are reviewed and the evidence for each discussed. Background information on biostratigraphy and taxonomy is also provided.

2.1 Biostratigraphy

The biozonal scheme of Koren' *et al.* (1996) has been used throughout the thesis. The scheme is given in Table 2.1. All zones have their bases defined on the first appearance of the index fossil, with the exception of the *spiralis* Zone, which is an interval biozone (Koren' *et al.* 1996). Some areas have more detailed zonal schemes, with separate *praedeubeli* and *deubeli* zones and sometimes subdivision of the *parvus-nassa* Zone, for example the scheme used in Germany by Jaeger (1991) (Table 2.2). In some areas separate *praedeubeli-deubeli* and *ludensis* zones have not been distinguished, for example in Britain only the *ludensis* Zone has been recognised above the *parvus-nassa* Zone (Holland *et al.* 1969; Warren 1971; Zalasiewicz & Williams 1999). Because recognition of separate *praedeubeli-deubeli* and *ludensis* zones is not always possible, in this thesis *ludensis* Zone *sensu stricto* means the *ludensis* Zone as defined by Koren' *et al.* (1996), and *ludensis* Zone *sensu lato* is used to mean a zone including both the *praedeubeli-deubeli* and *ludensis* zones.

Table 2.1: *Silurian graptoloid biozones, from Koren'* et al. *(1996).*

Period	**Series**	**Stage**	**Biozone**
Silurian	Přídolí		*bouceki-transgrediens*
			branikensis-lochkovensis
			parultimus-ultimus
	Ludlow	Ludfordian	*formosus*
			bohemicus tenuis-kozlowskii
		Gorstian	*leintwardinensis*
			scanicus
			nilssoni
	Wenlock	Homerian	*ludensis*
			praedeubeli-deubeli
			parvus-nassa
			lundgreni
		Sheinwoodian	*rigidus-perneri*
			riccartonensis-belophorus
			centrifugus-murchisoni
	Llandovery	Telychian	*lapworthi-insectus*
			spiralis interval
			griestoniensis-crenulata
			turriculatus-crispus
			guerichi
		Aeronian	*sedgwickii*
			convolutus
			argenteus
			triangulatus-pectinatus
		Rhuddanian	*cyphus*
			vesiculosus
			acuminatus
Ordovician	Ashgill		*persculptus*

Table 2.2: *Correlation of the scheme of Koren'* et al. *(1996) with that of Jaeger (1991).*

Koren' *et al.* 1996	**Jaeger 1991**
ludensis	*M. gerhardi* & *M. ludensis*
praedeubeli-deubeli	*M. deubeli*
	M. praedeubeli
parvus-nassa	*M. dubius/Ret. nassa* Interregnum
	M. dubius parvus
lundgreni	*Cyrtograptus lundgreni* zone, *M. testis* subzone

The zonal scheme of Koren' *et al.* (1996) for the late Homerian relies on the *Colonograptus ludensis* group (*C. deubeli, C. ludensis* and *C. praedeubeli*) as zonal fossils. However, in some areas the range of the C. *ludensis* group species overlap, for example the ranges of *C. praedeubeli*, *C. deubeli* and *C. ludensis* overlap in Arctic Canada (Lenz 1995) and China (Lenz *et al.* 1996; Zhang & Lenz 1997). This means that isolated occurrences of *C. praedeubeli* or *C. deubeli* could belong to either the *praedeubeli-deubeli* or the *ludensis* zones. Furthermore, some workers (e.g. Rickards & Wright 1997) consider that *C. praedeubeli* is an early growth stage of *C. ludensis*. An alternative zonal scheme for the late Homerian exists (Table 2.3), which recognises a *Lobograptus? sherrardae* Biozone, equivalent to the *praedeubeli* Zone (Rickards & Wright 1997), above the *parvus-nassa* Zone. This zonal scheme has been used in central Asia (e.g. Koren' 1991) and New South Wales (Rickards and Wright 1997), but has the potential to be used more widely, because *L*? *sherrardae* is found in Arctic Canada (Lenz 1995; Lenz & Kozłowska-Dawidziuk 2002a), New South Wales (Rickards & Wright 1997), central Asia (Koren' 1991, 1992; Koren' & Suyarkova 1994) and possibly in the Czech Republic (Kozłowska-Dawidziuk *et al.* 2001). However, this zonal scheme was not used in this thesis as *L*? *sherrardae* has not yet been found in many areas, for example North Africa, China and most of Europe.

Table 2.3: *Correlation of the zonal scheme of Koren'* et al. *1996) with that of Koren' (1992).*

Koren' *et al.* 1996	**Koren' 1992**
ludensis	*ludensis*
praedeubeli- deubeli	*deubeli*
	sherrardae (praedeubeli)
parvus-nassa	*nassa/dubius*
lundgreni	*lundgreni/testis*

The *parvus-nassa* Zone was originally called the *Gothograptus nassa* Interregnum (Jaeger 1991) and defined as an interval biozone, the time between the disappearance of the *lundgreni* Zone fauna and the appearance of the *ludensis* Zone fauna. Koren' *et al.* (1996) defined the base of the *parvus-nassa* Zone to be the first appearance of *Pristiograptus parvus*. The species commonly found in this zone are *Gothograptus* *nassa, Pristiograptus parvus* and *P. dubius*. However, these species are also known from the *lundgreni* Zone and/or the *ludensis* Zone *s.l.*, so this zone cannot be recognised with certainty except from sections that contain zones below and above the *parvus-nassa* Zone. (*P. dubius* is found in both the *lundgreni* and *ludensis s.l.* zones. *P. parvus* has been recognised in the *lundgreni* Zone (e.g. Kaljo *et al.* 1984). Koren' (1992) reported *G. nassa* from the *lundgreni* Zone; however, Lenz & Kozlowska-Dawidziuk (2001a) considered that all *lundgreni* Zone records of *G. nassa* were probably misidentifications of related species, although restudy of original material would be needed to confirm this.)

2.2 Taxonomy

The taxonomy of Homerian graptoloids has been extensively revised over the years. In particular the retiolitids have undergone substantial revision, especially by Anna Kozłowska-Dawidziuk and Alfred Lenz (e.g. Kozłowska-Dawidziuk 1990, 1995, Lenz & Kozłowska-Dawidziuk 2001a; 2002a). Some species have been placed in many different genera. For example, the retiolitid *Cometograptus nevadensis* has been placed in the following genera: *Retiolites* (e.g. Berry & Murphy 1975), *Plectograptus* (e.g. Koren' 1992), *Spinograptus* (e.g. Lenz 1995) and *Cometograptus* (e.g. Lenz & Kozłowska-Dawidziuk 2001a). Similarly, the monograptid *Colonograptus ludensis* has been assigned to the genera *Pristiograptus* (e.g. Berry & Murphy 1975) '*Pristiograptus*' (e.g. Lenz 1994a), *Monograptus* (e.g. Rickards *et al.* 1995a), *Colonograptus*? (e.g. Lenz 1995) and *Colonograptus* (e.g. Lenz & Kozłowska-Dawidziuk 2002a). To avoid confusion I have used the currently accepted taxonomy throughout, even when referring to papers that use older taxonomy. Cases of synonymy are explained in the text (sections 5.2.2.1 and 5.2.2.3). Authorships for species are given in Appendix 3, and therefore are not mentioned in the text except where a species is not in the appendix.

An outline of Homerian graptoloid taxonomy is given below, listing all the genera mentioned in this thesis. Monograptid family-level taxonomy is taken from Fortey &

Cooper (1986) and Melchin (1998); that for the retiolitids follows Kozłowska-Dawidziuk (2001). *Sagenograptus* Lenz & Kozłowska-Dawidziuk 2001a was not mentioned by Kozłowska-Dawidziuk (2001). It is assigned to the Plectograptinae here because of its possible descent from *Pseudoplectograptus sagenus* (Lenz & Kozłowska-Dawidziuk 2001a).

Many of the taxa listed below are not monophyletic, for example the subfamily Retiolitinae is paraphyletic and the Plectograptinae are polyphyletic, as defined by Kozłowska-Dawidziuk (2001, Figure 1). Within the monograptids, genera are not cladistically defined, many being paraphyletic and/or polyphyletic. In particular, the genus *Monograptus* is a dustbin taxon – the definition of *Monograptus* given in the *Treatise on Invertebrate Paleontology* is "Thecae and shape of rhabdosome variable, comprising all Monograptidae other than the genera recognised below" (Bulman 1970 p.V132). *Monograptus sensu stricto* is used only to refer to *priodon*-type hooked monograptids, but *Monograptus sensu lato* can refer to any monograptid whose generic position is unclear. Thus the classification used here should not be regarded as final, but instead as a working system.

- Order Graptoloidea Lapworth in Hopkinson & Lapworth 1875
  - Suborder Virgellina Fortey & Cooper 1986
    - Family Neodiplograptidae Koren' & Rickards 1996
        - Genus *Neoglyptograptus* Rickards *et al.* 1995a
    - Family Retiolitidae Lapworth 1873
      - Subfamily Retiolitinae Lapworth 1873
        - Genus *Eisenackograptus* Kozłowska-Dawidziuk 1990
        - Genus *Paraplectograptus* Přibyl 1948
        - Genus *Retiolites* Barrande 1850
      - Subfamily Plectograptinae Bouček & Münch 1952
        - Genus *Baculograptus* Lenz & Kozłowska-Dawidziuk 2002a
        - Genus *Cometograptus* Kozłowska-Dawidziuk 2001
        - Genus *Doliograptus* Lenz & Kozłowska-Dawidziuk 2002a

        - Genus *Gothograptus* Frech 1897
        - Genus *Papiliograptus* Lenz & Kozłowska-Dawidziuk 2002a
        - Genus *Plectograptus* Moberg & Törnquist 1909
        - Genus *Pseudoplectograptus* Obut & Zaslavskaya 1983
        - Genus *Sagenograptus* Lenz & Kozłowska-Dawidziuk 2001a
        - Genus *Sokolovograptus* Obut & Zaslavskaya 1976
        - Genus *Spinograptus* Bouček & Münch 1952
- Family Monograptidae Lapworth 1873
    - Subfamily Monograptinae Bouček 1933
        - Genus *Colonograptus* Přibyl 1942
        - Genus *Euroclimacis* Štorch 1998
        - Genus *Lobograptus* Urbanek 1958
        - Genus *Mediograptus* Bouček & Přibyl in Přibyl 1948
        - Genus *Monoclimacis* Frech 1897
        - Genus *Monograptus* Geinitz 1852
        - Genus *Pristiograptus* Jaekel 1889
        - Genus *Saetograptus* Přibyl 1942
        - Genus *Testograptus* Přibyl 1967
    - Subfamily Cyrtograptinae Bouček 1933
        - Genus *Cyrtograptus* Carruthers 1867

2.3 Extinction events

2.3.1 Recognition and classification of extinction events

Extinction events can be defined as either lows in taxon diversity or lows in taxon survivorship, where the taxon may be at any level. Clearly an extinction event at the family level will also be an event at the species level, but the converse is not necessarily true – there may be significant extinction at the species level but no family-level extinction at all. Most workers (e.g. Koren' 1987) have recognised extinction events as being lows in graptolite diversity. (For the purposes of this review, the diversity of a group in any particular time and/or place is the number of species of that group present in that time and/or place.) Melchin *et al.* (1998) used a different definition, defining extinction events as times when the percentage survivorship of species from one biozone to the next was less than 45.6% (one standard deviation from the mean of the survivorship rate). Using this definition of extinction event may lead to problems with pseudoextinction. For example, if a lineage evolves so rapidly that several species originate and become extinct within a single biozone the species survivorship will be low, but the lineage survivorship may be high - see Figure 2.1 below. Obviously an extinction event by the first definition will also be an extinction event by the second, but the converse is not necessarily true. The *lundgreni* event is an extinction event by both definitions.

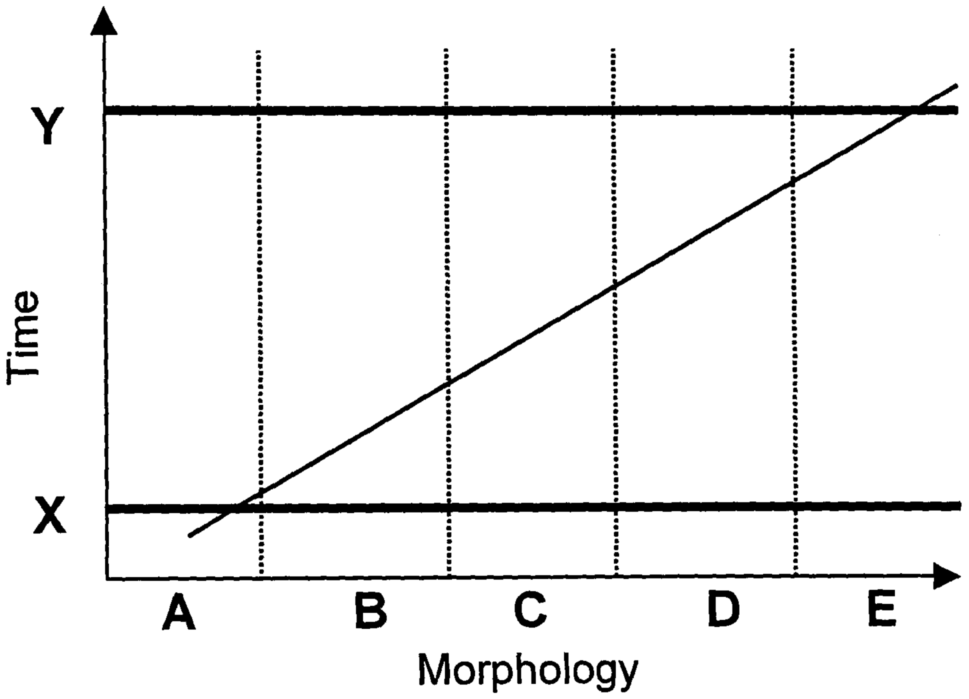


Figure 2.1: *A single continuous lineage evolves such that different parts of the lineage are given different species names (represented by the letters A to E). At the end of the time interval X to Y species A, B, C and D have apparently become extinct. However, no real extinction has occurred, as the single lineage still survives. The apparent species extinctions are an artefact caused by dividing the continuously evolving lineage into species.*

Obviously some extinction events are more severe than others, for example the end-Permian mass extinction (at least 75% of species extinct, perhaps more than 90% (Hallam & Wignall 1997 p.94)) was more severe than the Pleistocene extinctions (extinction rates did not exceed background extinction rates for most groups, with the notable exception of large mammals (Roy 2001)). Kaljo *et al.* (1996) defined a scale of extinction severity (Table 2.4). The smaller the event order, the higher the taxonomic rank affected. For example, a first order event might affect order level, but a fifth order event would only affect the species level. The *lundgreni* event is a third order event in this classification system (Kaljo *et al.* 1996, Figure 1).

Table 2.4: *Classification of bio-events from Kaljo* et al. *(1996).*

Event order	**Characteristics of event**
First	Mass extinction; comparable with the Ordovician-Silurian or Cretaceous-Tertiary extinctions
Second	Concurrent involvement of several groups in extinction and radiation processes, with a mass extinction in at least one group
Third	Prevailing extinction in several groups, mass extinction in one group or the final extinction of a family-level group
Fourth	Profound diversity change (extinction) or a clear innovation (at least at the genus level) in one or two groups
Fifth	Distinct diversity changes without any high level innovation in one or two groups

2.3.2 Graptoloid diversity during the Silurian

Silurian graptoloid diversity has been studied by many authors (e.g. Rickards 1977, 1978; Koren' 1987; Melchin *et al.* 1998; Urbanek 1993). At the species level there are many extinction events (Figure 2.2). Silurian and early Devonian extinction events are marked in Table 2.5. Details of the taxa becoming extinct during each event are provided in Tables 2.6 to 2.9 below, together with information about significant originations and radiations.

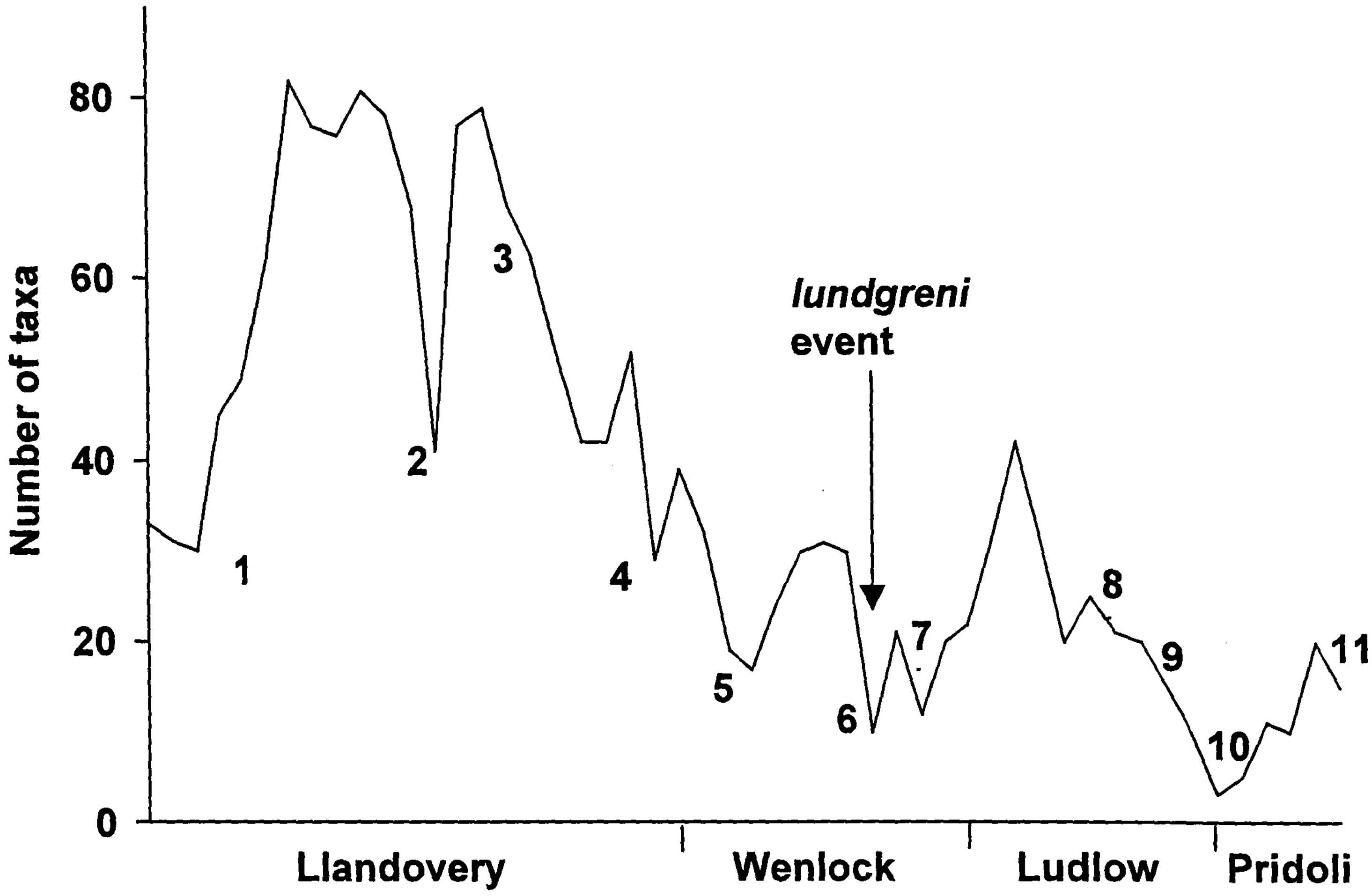


Figure 2.2: *Silurian graptoloid diversity, redrawn from Figure 4 of Melchin* et al. *(1998). Extinction events are marked by numbers. 1 =* acuminatus *event, 2 =* sedgwickii *event, 3 =* turriculatus *event, 4 =* lapworthi *event, 5 =* murchisoni *event, 6 =* lundgreni *event, 7 =* ludensis *event, 8 =* leintwardinensis *event, 9 =* kozlowskii *event, 10 =* formosus *event, 11 =* transgrediens *event.*

Peaks in graptoloid diversity occur during the Llandovery, Wenlock, early Ludlow, Přídolí and early Devonian. In general, diversity peaks occur when major structural changes evolve, such as the origin of triangulate monograptids in the *triangulatus* Zone (Rickards 1977). Major diversity lows occur during the late Wenlock, end Ludlow and end Přídolí. Graptoloids finally became extinct during the early Devonian. Overall, graptoloid diversity decreases during the Silurian. Most extinction events are recognised globally, with some exceptions. The *turriculatus* event (equivalent to the *utilis* event of Loydell 1994) has been seen in some parts of Europe but not in Arctic Canada or Denmark (Melchin *et al.* 1998), and an extinction event at the end of the *ludensis* Zone has been observed in the East Baltic (Kaljo & Märss 1991) and Canada (Lenz 1993a), but has not been recognised globally – no extinction event was recognised at this time by Melchin *et al.* (1998). Some of the extinction events in Figure 2.2, for example the *turriculatus* event, occur during a time when graptoloid diversity declines over several zones, and so are part of a medium- to long-term decrease in diversity. The *lundgreni* event is not of this type; diversity before the *lundgreni* event is relatively high, diversity declines within the zone and increases again shortly afterwards. Although global diversity after the *lundgreni* event is approximately ten species worldwide, the diversity seen in any one section is much lower than this.

Table 2.5: *Silurian and Devonian graptoloid extinction events. Silurian biozones from Koren'* et al. *(1996), Devonian from Koren' (1987). Extinction events from Kaljo & Märss (1991), Koren' (1979) and Melchin* et al. *(1998).*

Period	**Series**	**Stage**	**Biozone**	**Events**
Devonian	Lower Devonian	Pragian	*yukonensis*	*
			fanicus-falcarius	
		Lochkovian	*hercynicus*	*
			uniformis	
Silurian	Přídolí		*bouceki-transgrediens*	*
			branikensis-lochkovensis	
			parultimus-ultimus	
	Ludlow	Ludfordian	*formosus*	*
			bohemicus tenuis-kozlowskii	*
		Gorstian	*leintwardinensis*	*
			scanicus	
			nilssoni	
	Wenlock	Homerian	*ludensis*	*
			praedeubeli-deubeli	
			parvus-nassa	
			lundgreni	*
		Sheinwoodian	*rigidus-perneri*	
			riccartonensis-belophorus	
			centrifugus-murchisoni	*
	Llandovery	Telychian	*lapworthi-insectus*	*
			spiralis interval	
			griestoniensis-crenulata	
			turriculatus-crispus	*
			guerichi	
		Aeronian	*sedgwickii*	*
			convolutus	
			argenteus	
			triangulatus-pectinatus	
		Rhuddanian	*cyphus*	
			vesiculosus	
			acuminatus	*
Ordovician	Ashgill		*persculptus*	

Table 2.6: *Summary of graptoloid appearances, radiations and extinctions for the Ludlow, Přídolí and lower Devonian. Zones in which extinction events occur are marked in bold. 1 = Koren' 1987, 2 = Koren' 1979, 3 = Melchin* et al. *1998, 4 = Urbanek & Teller 1997, 5 = Kaljo* et al. *1996, 6 = Urbanek 1993.*

Series	Zone	Appearances	Radiations	Extinctions
Lower Devonian	***yukonensis***			All remaining graptoloids
	fanicus-falcarius			
	hercynicus	*Abiesgraptus* (1)		Multiramous linograptids (2)
	uniformis	*Monograptus uniformis* and *Monograptus aequabilis* groups (1)		
Přídolí	***bouceki-transgrediens***			*Pseudomonoclimacis, Pristiograptus* (3)
	branikensis-lochkovensis			
	parultimus-ultimus			
Ludlow	***formosus***	*Monograptus formosus* group and others (1)		Lobate-spinose monograptids (4)
	bohemicus tenuis-kozlowskii	*Neolobograptus, Neocucullograptus* (1)		*Neolobograptus, Bohemograptus, Polonograptus, Neocucullograptus* (5)
	leintwardinensis	Subfamily Linograptinae (Koren' 1987)	*Monograptus uncinatus* group (1)	Plectograptines (3, 6), *Saetograptus, Cucullograptus aversus* group (6)
	scanicus		Lobograptids (1)	
	nilssoni	*Bohemograptus, M.uncinatus* group, *Saetograptus, Neodiversograptus* (1)		

Table 2.7: *Summary of graptoloid appearances, radiations and extinctions for the Wenlock. Zones in which extinction events occur are marked in bold.*

Series	Zone	Appearances	Radiations	Extinctions
Wenlock	***ludensis***	Common ancestor of the subfamilies Linograptinae, Cucullograptinae, Neocucullograptinae (Koren' 1987)	*Pristiograptus dubius* group, subfamily Plectograptinae (Koren' 1987)	
	praedeubeli-deubeli			
	parvus-nassa			
	lundgreni		Cyrtograptids (Koren' 1987)	*Cyrtograptus* (Lenz 1994b), monograptids of the *vomerina*, *priodon-flemingii* and *exiguus* groups (Urbanek 1993)
	rigidus-perneri			
	riccartonensis-belophorus	Subfamily Plectograptinae, new cyrtograptid lineages (Koren' 1987)		
	centrifugus-murchisoni			*Barrandeograptus, Cyrtograptus murchisoni* group (Melchin *et al.* 1998)

Table 2.8: *Summary of graptoloid appearances, radiations and extinctions for the Aeronian and Telychian (Llandovery). Zones in which extinction events occur are marked in bold. 1 = Melchin* et al. *1998, 2 = Koren' 1987, 3 = Loydell 1994, 4 = Koren' & Rickards 1996.*

Series	Zone	Appearances	Radiations	Extinctions
Llandovery	***lapworthi-insectus***			*Oktavites* and *Torquigraptus* extinct. *Cyrtograptus*, *Diversograptus* and *Streptograptus* much reduced (1)
	spiralis interval			
	griestoniensis-crenulata	Cyrtograptidae (2)		
	turriculatus-crispus	*Sinodiversograptus*, *Retiolites geinitzianus* group, *Monograptus priodon* group, *Monograptus spiralis* group (= *Oktavites*), *Pristiograptus dubius* group (2)		Retiolitids, biserials, rastritids badly affected (3)
	guerichi			
	sedgwickii			Pseudorthograptids extinct, *Campograptus*, *Coronograptus*, *"Demirastrites"* and *Rastrites* badly affected (1)
	convolutus		Speciation in *Petalolithus folium* lineage (4)	
	argenteus			
	triangulatus-pectinatus	*Rastrites*, *Petalolithus*, *Diversograptus* and other genera (2)	Triangulate monograptids (2)	

Table 2.9: *Summary of graptoloid appearances, radiations and extinctions for the latest Ordovician and the Rhuddanian (Llandovery). Zones in which extinction events occur are marked in bold.*

Series	**Zone**	**Appearances**	**Radiations**	**Extinctions**
Llandovery	*cyphus*	*Metaclimacograptus, Clinoclimacograptus* and *Rhaphidograptus* (Koren' 1987). In S. Urals, pseudorthograptids and rivagraptids (Koren' & Rickards 1996)	"Stem" atavograptids – *Pribylograptus, Lagarograptus* and *Coronograptus* (Koren' 1987), in S. Urals, radiation in glyptograptids (Koren' & Rickards 1996)	
	vesiculosus		Beginning of monograptid radiation (continues until *triangulatus* Zone) (Koren' & Bjerreskov 1999)	*Akidograptus* and *Parakidograptus* present at the base of this zone (Melchin *et al.* 1998)
	acuminatus			*Hirsutograptus*, species of *Normalograptus, Neodiplograptus, Cystograptus* and *Atavograptus* (Melchin *et al.* 1998)
Ashgill	*persculptus*	Monograptids (Koren' 1987), *Akidograptus, Parakidograptus* (Melchin *et al.* 1998)	Diplograptid radiation (Koren' & Bjerreskov 1999)	

2.3.3 General patterns in extinction events

Silurian graptoloid extinction events tend to have two things in common: firstly, that the survivors of extinction events tend to be taxa with simple morphology, and secondly, that graptoloids occurring immediately after extinction events tend to be small. These are discussed separately below.

In general, taxa with more complex morphologies become extinct during extinction events, for example *Rastrites* in the *sedgwickii* and *turriculatus* events and cyrtograptids in the *lundgreni* event. Taxa with simple morphology tend to survive, such as the *Pristiograptus dubius* group in the *lundgreni*, *leintwardinensis* and *kozlowskii* events (Urbanek 1993), and small taxa, such as *Normalograptus* at the end-Ordovician extinction (Melchin & Mitchell 1991). The genus *Pristiograptus*, which has simple thecae, is one of the longest-lasting graptoloid genera, originating in the Llandovery *acinaces* Zone (Rickards 1976, equivalent to the lower part of the *cyphus* zone of the Koren' *et al.* (1996) scheme) and becoming extinct twenty-four zones later in the *bouceki-transgrediens* Zone (Melchin *et al.* 1998).

Several workers have noticed that taxa immediately after extinction events tend to be small – Urbanek (1993) called this the "Lilliput Effect." For example, Bates & Kirk (1984) noticed this for taxa after the Ordovician mass extinction, Loydell (1994) for *Streptograptus johnsonae* after the *turriculatus* event, and Urbanek (1993) for *Pristiograptus parvus* after the *lundgreni* event. Various explanations have been advanced for the Lilliput Effect. Urbanek (1993) argued that the effect was ecophenotypic, caused by stunting. Jaeger (1991) suggested that the effect might be due to a mutation for small size which gave its possessors a selective advantage in disturbed conditions, which were replaced by more normal morphs when conditions became less disturbed. Berry & Hartman (1998) attributed the small size of graptoloids and the origin of dimorphograptids and monograptids after the Ordovician mass extinction to horizontal gene transfer between lineages. (Horizontal gene transfer is the insertion of genes from one lineage into another, unrelated, lineage by viruses or viroids (Berry & Hartman 1998)). The same mechanism was invoked by Jeppsson (1986) as a possible explanation for some cases of convergent evolution in conodonts. This idea is unfortunately untestable, as graptoloid DNA is unlikely to be found - the time limit for DNA recovery is about 100 000 years (Poinar & Pääbo 2001). Another possible explanation for the Lilliput Effect is that species with a large body size become extinct during extinction events more readily than those with a small body size, so the only species present after an extinction event are small ones. (Large body size has been shown to increase extinction likelihood in many, but not all, groups (McKinney 2001)). These hypotheses could be tested by looking at body sizes in the same species or species group before, during and after an extinction event. If the hypotheses of Urbanek (1993) or Jaeger (1991) are correct, body size will be smaller immediately after the event. If the hypothesis that large species preferentially become extinct is correct, body size of a species will not change.

2.4 The *lundgreni* extinction event

The *lundgreni* event is the most severe of the early Silurian extinction events in terms of percentage extinction, termination of lineages and subsequent low diversity (Melchin *et al.* 1998). An event at this time has been seen in acritarchs (Kaljo *et al.* 1996; Masiak 1999), and chitinozoans also experience an extinction event during the *lundgreni* Zone (Kaljo *et al.* 1996; Nestor 1992), but the event does not seem to have affected the benthos (Boucot 1990). The extinction occurs at the end of the *lundgreni* Zone, and appears to have been sudden (Berry 1995), at least in some areas. However, in Central Asia the number of cyrtograptid species declines in a stepwise manner before the end of the *lundgreni* Zone, whereas all the monograptid species last until the end of the zone (Koren' 1991). Diversity is low during the *parvus-nassa* Zone, with mass occurrences of *Pristiograptus parvus* and *Gothograptus nassa* (Jaeger 1991). Recovery from the extinction begins in the *praedeubeli-deubeli* and *ludensis* zones, with the appearance of the *Colonograptus ludensis* and *Lobograptus? sherrardae* groups (Koren' & Urbanek 1994) and a radiation of retiolitids (Koren'

1987; Kozłowska-Dawidziuk *et al.* 2001). These groups are thought to have originated from *Pristiograptus dubius* and *Gothograptus* (Koren' & Urbanek 1994; Kozłowska-Dawidziuk 2001).

It has been stated by some authors that only *Pristiograptus dubius* and *Gothograptus* survive the *lundgreni* event (e.g. Kaljo *et al.* 1996; Koren' 1991; Lenz & Kozłowska-Dawidziuk 2001a), but there are many records of other taxa surviving, recently reviewed by Rickards & Wright (2001). *Monograptus sensu stricto* (*priodon*-type hooked monograptids) is abundant in the *lundgreni* Zone (*M. flemingii* is found worldwide), and the morphology reappears in the lower Ludlow (the *M. uncinatus* group, Urbanek 1998). There are rare occurrences of *Monograptus s.s.* in the *praedeubeli-deubeli* and *ludensis* zones of Britain, Australia and Alaska (Warren *et al.* 1984; Rickards *et al.* 1995a; Churkin & Carter 1996), but studies in Arctic Canada, continental Europe and Central Asia have failed to establish the presence of hooked monograptids at this level (Lenz & Kozłowska-Dawidziuk 2001b). *Cyrtograptus* and *Testograptus* become extinct at the end of the *lundgreni* Zone in most of the world (Lenz 1994b; Koren' 1987; Urbanek 1993), but are found after this time in Australia (Rickards *et al.* 1995a). *Monoclimacis* is also said to have died out during the *lundgreni* event (Koren' 1987), but a Wenlock-style *Monoclimacis* (*Mcl. ludlowensis* Rickards *et al.* 1995a) has been reported from the Ludlow of Australia, although its exact ancestry is uncertain (Rickards *et al.* 1995a). Reports from the literature of graptoloids surviving the *lundgreni* event are summarised in Tables 2.10 and 2.11. All these occurrences are from small areas, not widespread, so these survivors are extremely rare. The only records of retiolitid survivors (apart from the ubiquitous *Gothograptus nassa*) are from Arctic Canada. This probably reflects the fact that retiolitids are more easily studied in isolated material, and this is rare during the Homerian, occurring only in Arctic Canada, Poland and Sweden. Of the graptoloids that survive the *lundgreni* event, *Cyrtograptus* and *Testograptus* do not re-radiate and are assumed to become extinct early in the Ludlow.

Table 2.10: *Monograptid survivors of the* lundgreni *event.* Cyrt. = Cyrtograptus, Mcl. = Monoclimacis, M. = Monograptus, P. = Pristograptus, T. = Testograptus.

Species	**Place**	**Reference**	**Notes**
Cyrt. ex gr. cf. *ellesae*	New South Wales	Rickards *et al.* 1995a	Occurs in lower Ludlow
Mcl. ludlowensis	New South Wales	Rickards *et al.* 1995a	Wenlock-style monoclimacid in *nilssoni* Zone
M. aff. *priodon*	Alaska	Churkin & Carter 1996	
M. cf. *M. uncinatus micropoma*	Alaska	Churkin & Carter 1996	
M. flemingii	New South Wales	Jenkins 1978	
M. flemingii aff. *elegans*	North Wales	Warren 1971; Warren *et al.* 1984	
M. moorsi	New South Wales	Rickards & Wright 1997	*Monograptus s.s.* in *sherrardae* Subzone (equivalent to *praedeubeli-deubeli* Zone)
M. sp. ex gr. *flemingii*	New South Wales	Rickards *et al.* 1995a	This record has been disputed by Lenz & Kozłowska-Dawidziuk (2001a)
P. jaegeri	UK	Holland *et al.* 1969	*P. jaegeri* is also known from other places in the *lundgreni* Zone, and is widespread in the *praedeubeli-deubeli* and *ludensis* zones
P. pseudodubius	North Wales	Warren 1971; Warren *et al.* 1984	Occurs *rigidus* to *ludensis* zones
P. sp. nov. aff. *curtus*	North Wales	Warren 1971; Warren *et al.* 1984	Occurs *lundgreni* to *nilssoni* zones
T. testis	New South Wales	Rickards *et al.* 1995a	*ludensis* Zone *s.l.*
T. testis	Arctic Canada	Lenz & Melchin 1991	Table 8 shows *T. testis* appearing with *Colonograptus ludensis*

Table 2.11: *Retiolitid survivors of the* lundgreni *event.*

Species	**Place**	**Reference**
Eisenackograptus eisenacki	Arctic Canada	Lenz 1993b
Spinograptus clathrospinosus	Arctic Canada	Lenz 1993b

The records of *Baculograptus chainos* and *Cometograptus nevadensis* reported by Lenz & Melchin (1991) and Lenz (1995) from after the *lundgreni* event in Arctic Canada are not the taxa stated, but new species, hence are not extinction survivors (Lenz & Kozłowska-Dawidziuk 2001a).

Rickards *et al.* 1995a figured four specimens named as *Monograptus* sp. ex gr. *flemingii* from the *ludensis* Zone of Quarry Creek, New South Wales. However, these identifications were queried by Lenz & Kozłowska-Dawidziuk (2001b, 2002b), who examined some of the specimens and re-interpreted them as "some type of badly deformed pristiograptid." This is discussed further in Section 4.3.

Warren (1971) and Warren *et al.* (1984) recorded *Monograptus flemingii* aff. *elegans* from the *ludensis* Zone of North Wales. I have examined specimens of *Monograptus flemingii* from that area in the British Geological Survey collections in Keyworth. The specimens I saw are definitely *M. flemingii*, but I do not know whether or not the specimens I looked at were those from the *ludensis* Zone - the specimens were labelled only as 'Homerian'.

Taxa after the *lundgreni* event are small, but some species before the event are large. *Pristiograptus parvus* and *Gothograptus nassa* are both small species, of the order of a centimetre or two in length. Some of the species in the *lundgreni* Zone, such as *Monograptus flemingii* and cyrtograptids, can be tens of centimetres long (Bulman 1965; Burns & Rickards 1993). This agrees with the general pattern of Silurian extinction events (Section 2.3.3).

2.5 Palaeogeography and biogeography

2.5.1 Palaeogeography

The palaeogeographic map used is that of Scotese (2001) (Figure 2.3). Graptoloids are found in most areas except for southern Gondwana (present-day South America and southern Africa) and Antarctica. Homerian graptoloid distribution is discussed further in Chapter 5. Alternative palaeogeographical reconstructions exist for the Wenlock, for example that of Torsvik *et al.* (1996). The Torsvik *et al.* and Scotese maps differ slightly. The Scotese map shows the Bohemian massif (present-day Czech Republic) and the Armorican-Iberian massifs (modern France, Spain and Portugal) as being attached to North Africa. The Torsvik reconstruction shows these places as being separate continental blocks in the Rheic Ocean, but still closer to Gondwana than to Laurentia. The differences between the maps are not significant for the purposes of this thesis. The Torsvik reconstruction was not used because it does not include all graptolite-bearing areas, for example it does not include Kazakhstania or Australia.

2.5.2 Graptoloid biogeography

In the Ordovician there are two distinct graptoloid faunal provinces: the Atlantic realm and the Pacific realm, with graptoloid distribution controlled by depth and to an extent by temperature (Cooper *et al.* 1991). In the Silurian endemism is less pronounced. In the Silurian three provinces have been recognised in the Llandovery and Wenlock (Rickards *et al.* 1990; Štorch 1996), and Ludlow faunas are cosmopolitan (Berry & Wilde 1990). In the Wenlock, Rickards *et al.* (1990) recognised the Pacific province (most faunas), the Rheic subprovince (Poland, Bohemia, Romania, Scandinavia and the Baltic region) and the Mediterranean Subprovince (North Africa, Spain, Portugal, Southern France, the Pyrenees and Sardinia). Some areas have endemic faunas in the late Homerian: endemic monograptids occur in central Asia (Koren' 1991) and the Sahara (Legrand 1994).

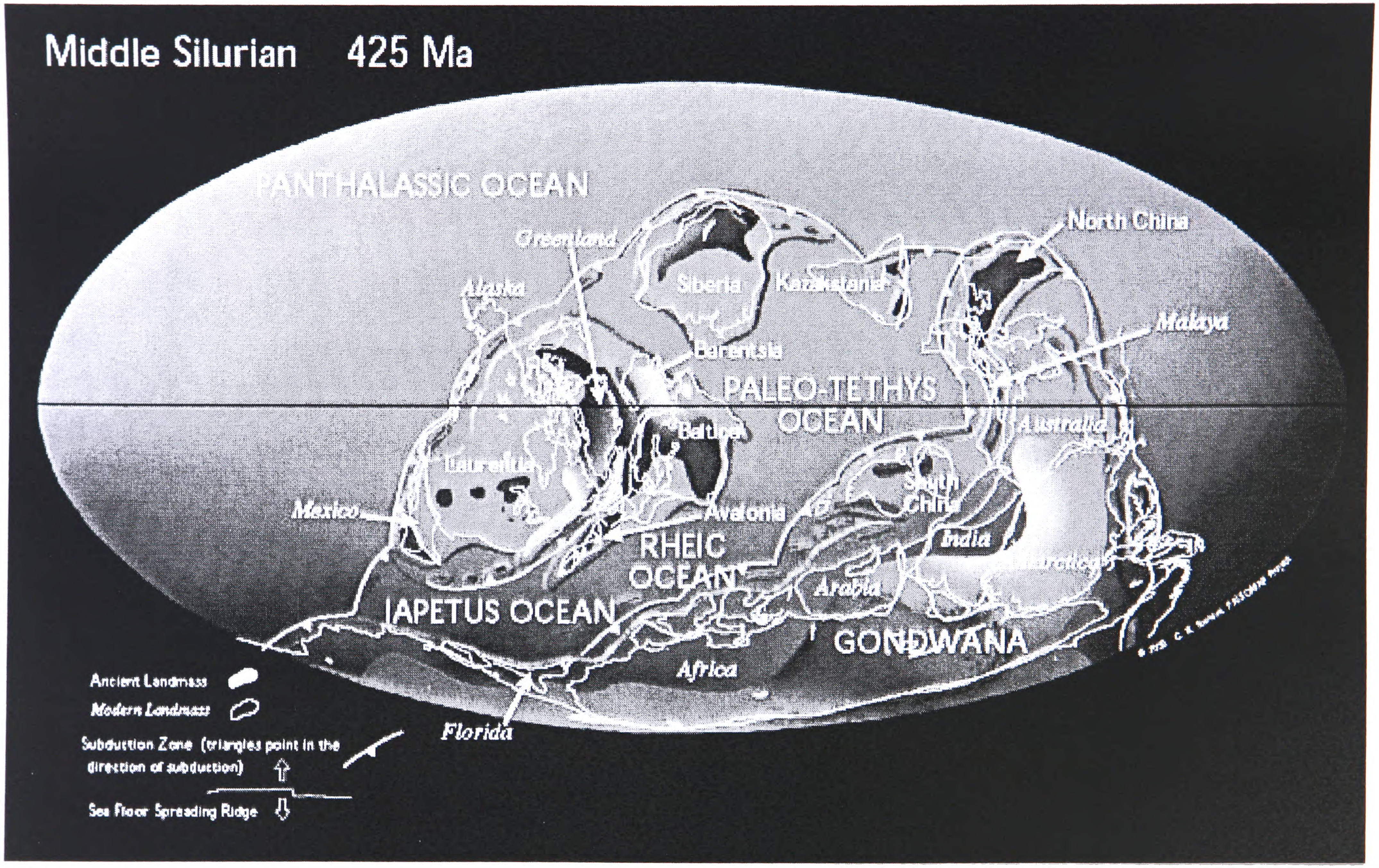


Figure 2.3: *Silurian palaeogeography. From the Paleomap project (www.scotese.com).*

The "Mediterranean graptolite fauna," which consists of graptoloids with extremely large rhabdosomes, has been recognised in the Wenlock of the Mediterranean region. This fauna is found in Sardinia, the Iberian Peninsula, North Africa, the Balkans, Turkey, France and the Alps (Romariz *et al.* 1972; Degardin 1981), and consists of wide rhabdosomes (more than a centimetre wide) with few thecae per centimetre, and narrower rhabdosomes with many thecae per centimetre (Romariz *et al.* 1972). This fauna is thought to be due to tectonic deformation of species known from other places (Jaeger 1976; Destombes *et al.* 1984).

2.6 Depth zonation

It has been known for many years that graptoloid diversity increases from shallower to deeper water (Elles 1939; Kaljo 1978). Further research has shown that diversity decreases again towards the open ocean (Finney & Berry 1997; Goldman *et al.* 1999). The idea that graptoloids may have been depth stratified was suggested by Berry (1962) and tested by Berry & Boucot (1972a), using the occurrences of graptoloids in shelly benthic communities. They detected depth zonation in late Llandovery graptoloids, with cyrtograptids occurring in deeper water and the *Monograptus priodon* group and retiolitids in shallower water. Depth zonation has also been detected for graptoloids in the Ordovician (Cooper *et al.* 1991). The idea was refined by Finney & Berry (1997) and Goldman *et al.* (1999), who found that depth stratification and lateral water mass specificity were both important, with the most diverse graptoloid fauna occurring in the nutrient-rich waters along the continental margin and less diverse faunas in shallower water and the open ocean.

It has been suggested that deeper-water graptoloids tend to become extinct during extinction events, and species living in shallower water tend to survive (Bates & Kirk 1984; Quinby-Hunt & Berry 1991). Cooper (1996) reported that deep-water Ordovician graptoloid species had an average lifespan that was less than half that of shallow-water taxa, 2.2 million years and 5.3 million years respectively. In the

Silurian, Berry & Boucot (1972a) stated that shallower-water species (the *Monograptus priodon* group, which includes *M. flemingii*) appeared to survive the longest, with the exception of *Pristiograptus*, which was found in deeper water but did survive for a long time. Quinby-Hunt & Berry (1991) say that the graptolites that went extinct in the *lundgreni* event lived in deeper water, with only shallow-water species surviving.

In order to test the hypothesis that shallow-water species survived the *lundgreni* event while deeper ones became extinct, information on depth zonation in *lundgreni* Zone graptoloids is required. If graptoloids were depth stratified, then there should be differences in the assemblages across basins, so data on the assemblages present across a basin from shorewards to oceanwards are needed. These data are available for the Welsh Basin and for Arctic Canada.

Although there are fewer species in the *lundgreni* Zone of the Welsh Basin than in some places, there is over a century of study of the faunas to draw upon, and the palaeogeography is well known. A list of the species found at three different localities in the *lundgreni* Zone is given in Table 2.12. Only monograptids have been included, as there are few retiolitid species known from the area. This may reflect collecting bias, as there are no isolatable faunas, or retiolitids may be genuinely rare in the area. Information on water depth is taken from Figure S3b of Bassett *et al.* (1992). The number of taxa is similar for each locality, and most species are found both in shallower and deeper water. Of the species found in shallower but not deeper water, most are slender species, so their absence from deeper water could be a result of taphonomic processes, but this seems unlikely as other fragile species, such as *Cyrt. lundgreni*, are found in Denbighshire. The absence of *Testograptus testis* from Denbighshire is unlikely to be due to collecting failure, as *T. testis* is a robust and distinctive species.

Table 2.12: *List of monograptid species found at various localities in the* lundgreni *Zone of the Welsh Basin. Species in bold are found both in shallower and deeper water.* C. = Colonograptus, Cyrt. = Cyrtograptus, Mcl. = Monoclimacis, Med. = Mediograptus, M. = Monograptus, P. = Pristiograptus, T. = Testograptus.

Locality	Builth Wells	Long Mountain	Denbighshire
Reference	Zalasiewicz & Williams 1999	Elles 1900; Palmer 1972	Warren 1971
Water depth	Shallower	Shallower	Deeper
Species present	***Cyrt. ellesae*** ***Cyrt.* cf. *hamatus*** ***Cyrt. lundgreni*** ***Cyrt.* cf. *perneri*** *Cyrt. ramosus* *Cyrt. urbaneki* ***Mcl. flumendosae*** ***P.* ex gr. *dubius*** *Med.* ex gr. *retroflexus*	***Cyrt. hamatus*** ***Cyrt. lundgreni*** ***Mcl. flumendosae*** ***M. flemingii*** *M. irfonensis* ***P. dubius*** ***P. pseudodubius*** *T. testis*	C. aff. *deubeli* ***Cyrt. ellesae*** ***Cyrt. hamatus*** ***Cyrt. lundgreni*** ***Cyrt. perneri*** ***Mcl. flumendosae*** ***M. flemingii*** ***P. dubius*** *P. lodenicensis* ***P. pseudodubius***
Number of species	9	8	10

The Homerian graptoloids of the Canadian Arctic have been well studied in recent years by Lenz and co-workers. The graptoloids considered here are from both near the shelf edge (Cornwallis, Devon and Hoved Islands) and from deeper water (Bathurst and Melville Islands) (Lenz & Kozłowska-Dawidziuk 2002a). Graptoloids are found both flattened and preserved in nodules (Lenz & Kozłowska-Dawidziuk 2002a). The shallower-water faunas have been studied more than those from deeper-water, because graptolite-bearing nodules are more common in the shallower deposits (Lenz & Kozłowska-Dawidziuk 2002a). The difference in the taphonomy of the deposits leads to a difficulty in finding some species, especially retiolitids, which are easily overlooked in flattened material. An idea of the scale of the problem could be gained by comparing the faunas known in flattened form from shallow and deep rocks, although there would still be a problem because the shallower-water beds have been sampled more extensively than the deeper-water deposits. This taphonomic/collector bias leads to problems when analysing the depth zonation. Clearly the number of species at different points in the basin means very little, as some parts of the basin have been better sampled than others. More species have been found on Cornwallis Island than anywhere else, but this may just be the result of sampling bias. Similarly, the fact that some species have been found on Cornwallis Island and not elsewhere probably reflects sampling bias.

Lists of the species found during and after the *lundgreni* Zone are given in Tables 2.13 to 2.16. In the *lundgreni* Zone, at the shelf edge there are thirteen retiolitid and sixteen monograptid species (one *Pristiograptus*, five *Cyrtograptus*, eight *Monograptus s.l.* and two *Monoclimacis*). Away from the shelf edge there are one retiolitid and six monograptid species (two *Monograptus*, one *Monoclimacis* and three *Cyrtograptus*). All of the species found away from the shelf edge are also found near the shelf edge. *Pristiograptus dubius* and *Testograptus testis* are not found away from the shelf edge. This is unlikely to be due to preservational or collector bias, as both species are robust and distinctive. This implies that these species were wholly or partly confined to shallow water. After the *lundgreni* Zone thirteen retiolitid and ten monograptid species are found near the shelf edge, and six retiolitid and seven monograptid species away from the shelf edge. Again, all of the species found away from the shelf edge are also found near the shelf edge.

In conclusion, at present there is little evidence for depth stratification in the Homerian of the Canadian Arctic, but further studies of the faunas away from the shelf edge are needed. In Wales there are minor differences between the shallow- and deep-water faunas. Neither location shows an increase in diversity from onshore to offshore. For Canada, this is probably an artefact of shelf-edge faunas being studied more intensively than those further basinwards. For Wales, this may be because of low diversity in the entire basin – many species found elsewhere are not found in Wales. Evidence from both Arctic Canada and Wales suggests that *Testograptus testis* is a shallow-water species.

As stated above, some authors (Bates & Kirk 1984; Quinby-Hunt & Berry 1991) have suggested that deeper-water species became extinct during the *lundgreni* event, with shallow-water species surviving. The evidence here does not tend to support this notion, as many taxa found in shallow water become extinct, for example *Testograptus testis*, *Cyrtograptus* and *Monograptus flemingii*, and some taxa which survive the event are found in deeper water, e.g. *Pristiograptus dubius*.

Table 2.13: Lundgreni *Zone retiolitids, Canadian Arctic. Data from Lenz 1993b, 1994c; Lenz & Kozłowska-Dawidziuk 2001a; Lenz & Melchin 1990, 1991. Records of aff., cf. or sp. have not been included.* Ag. = Agastograptus, Com. = Cometograptus, Eis. = Eisenackograptus, Para. = Paraplectograptus, Pseud. = Pseudoplectograptus, Ret. = Retiolites, Sag. = Sagenograptus, Sok. = Sokolovograptus, Spin. = Spinograptus.

	Near shelf edge		**Away from shelf edge**
Locality	Cornwallis Island	Devon Island	Bathurst Island
Species	*Ag. clathrospinosus* *Com. apoxys* *Com. apsis* *Com. kirki* *Com. marsupium* *Com. nevadensis* *Eis. eisenacki* ***Para. eiseli*** *Para. praemacilentus* *Plect. (Sok.) textor* *Pseud. praemacilentus* *Pseud. sagenus* *Pseud. simplex* *Ret. australis?* *Sag. arctos* *Spin. nevadensis*	*Com. nevadensis*	***Para. eiseli*** *Para. sp.*

Table 2.14: Lundgreni *Zone monograptids, Canadian Arctic. Data from Lenz 1993b, 1994c; Lenz & Kozłowska-Dawidziuk 2001a; Lenz & Melchin 1990, 1991. Records of aff., cf. or sp. have not been included.* Cyrt. = Cyrtograptus, E. = Euroclimacis, M. = Monograptus, Mcl. = Monoclimacis, P. = Pristiograptus, T. = Testograptus.

	Near shelf edge		**Away from shelf edge**	
Locality	Cornwallis Island	Devon Island	Bathurst Island	Melville Island
Species	***Cyrt. hamatus*** *Cyrt. lundgreni* ***Cyrt. multiramis*** *Cyrt. perneri* ***Cyrt. radians*** *M. firmus festinolatus* ***M. flemingi*** *M. instrenuus* *M. opimus* ***M. priodon*** *M? antennularius* *M? biglossa* ***Mcl. flumendosae*** *Mcl. simplex* *P. dubius* *T. testis*	*T. testis*	***Cyrt. multiramis*** ***M. flemingi*** ***Mcl. flumendosae***	***Cyrt. hamatus*** ***Cyrt. radians*** ***M. flemingi*** ***M. priodon*** ***Mcl. flumendosae***

Table 2.15: *Post*-lundgreni *Zone retiolitids, Canadian Arctic. Records of aff., cf. or sp. have not been included. Data from Lenz 1995; Lenz & Kozłowska-Dawidziuk 2002a.* Ag. = Agastograptus, Bac. = Baculograptus, Com. = Cometograptus, Dol. = Doliograptus, G. = Gothograptus, Pap. = Papiliograptus, Plect. = Plectograptus, Sok. = Sokolovograptus, Spin. = Spinograptus.

	Near shelf edge		**Away from shelf edge**
Locality	Cornwallis Island	Hoved Island	Bathurst Island
Species	*Plect. robustus* *Ag. wimani?* *Bac. batesi* ***Bac. chainos*** ***Spin. clathrospinosus*** ***"Spin." karlsteinensis*** ***Spin. latespinosus*** *Dol. latus* ***G. nassa*** *Pap. papilio* *Pap.? petilus* *Spin. praerobustus* *Spin. spinosus*	***Spin. clathrospinosus*** ***Plect. macilentus*** *Com. nevadensis*	***Bac. chainos?*** ***Spin. clathrospinosus*** ***"Spin." karlsteinensis*** ***Spin. latespinosus?*** ***G. nassa*** ***Plect. macilentus***

Table 2.16: *Post*-lundgreni *Zone monograptids, Canadian Arctic. Species in bold occur both near and away from the shelf edge. Records of aff., cf. or sp. have not been included. Data from Lenz 1995; Lenz & Kozłowska-Dawidziuk 2002a.* Co. = Colonograptus, L. = Lobograptus, Mcl. = Monoclimacis, P. = Pristiograptus.

	Near shelf edge		**Away from shelf edge**
Locality	Cornwallis Island	Hoved Island	Bathurst Island
Species	***Co. deubeli*** ***Co. ludensis*** ***Co. praedeubeli*** ***Co. schedidoneus*** *L.? claudiae* *L.? cornuatus* ***L.? sherrardae*** ***P. dubius*** *P. jaegeri*	***Co. deubeli*** ***Co. ludensis*** ***Co. praedeubeli*** ***Co. schedidoneus*** ***L. angustus*** *L.? claudiae* *L.? cornuatus* ***L.? sherrardae***	***Co. deubeli*** ***Co. ludensis*** ***Co. praedeubeli*** ***Co. schedidoneus*** ***L. angustus*** ***L.? sherrardae*** ***P. dubius***

2.7 The causes of graptoloid extinctions

A number of hypotheses have been proposed for the cause of the *lundgreni* event, including bolide impact, sea level change, expansion of anoxia, retreat of anoxia and changes in nutrient levels. These ideas are discussed below. It is difficult to identify a single cause of extinction events, as many factors that may affect diversity are inter-related. For example, sea level lowstands are correlated with positive $\delta^{13}C$ excursions, lack of graptolitic shale deposition and extinction events (Kaljo *et al.* 1998; Melchin *et al.* 1998).

2.7.1 Bolide impact

Berry *et al.* (1988) put forward the hypothesis that the *lundgreni* extinction, the development of massive carbonate reefs and the origin of vascular land plants in the late Wenlock may all have been caused by the impact of a bolide containing high levels of ammonia. The ammonia would have increased the pH of the oceans and the level of nutrients in the oceans and on land. The increase in nutrient levels would have increased primary productivity, allowing massive carbonate buildups in the sea and encouraging the development of vascular tissue on land. The increased pH would have encouraged the precipitation of carbonate and also may have been toxic to plankton. However, a global increase in pH severe enough to kill plankton would also have been severe enough to have affected the benthos, and there is no evidence for extinctions in benthos at this time. Also, there is no evidence for an impact at the end of the *lundgreni* Zone in that there is no trace of an iridium anomaly (Quinby-Hunt & Berry 1991), although a volatile bolide might not contain high levels of iridium.

2.7.2 Sea level changes

Diversity and sea level are correlated for many groups, diversity being greatest at times of high sea level and least when sea level is low. This pattern has been seen in ammonoids (Becker 1993; House 1993), ammonites (Sandoval *et al.* 2001), chitinozoans (Paris & Nõlvak 1999), gastropods (Gubanov 1998), calcareous nannoplankton (Roth 1987), trilobites (Zhou *et al.* 2000) and Ordovician graptoloids (Erdtmann 1986). Table 2.17 shows sea level changes at the time of graptoloid extinction events. Most extinction events are correlated with regressions, but some are not, for example the Wenlock *centrifugus-murchisoni* event and the final extinction of graptoloids in the Devonian, which occurred during a transgression (Koren' 1987). The *lundgreni* event is correlated with a regression (Melchin *et al.* 1998). However, sea level fall is not thought to be the cause of extinction events, but instead to be correlated with some other factor that causes extinction (Melchin *et al.* 1998).

Table 2.17: *Sea level changes at the time of graptoloid extinction events (Melchin* et al. *1998).*

Extinction event	**Sea level**
bouceki-transgrediens	Regression
formosus	Transgression
bohemicus tenuis-kozlowskii	Regression
leintwardinensis	Regression
lundgreni	Regression
centrifugus-murchisoni	Transgression
lapworthi-insectus	Regression
turriculatus-crispus	Regression
sedgwickii	Regression
acuminatus	In the middle of an overall trangression

Work by Smith *et al.* (2001) and Peters & Foote (2002) indicates that the apparent correlation of sea level changes and extinctions may be an artefact of the sedimentary record. During a transgression, condensed sedimentary successions form on cratons and are subsequently destroyed by erosion. The shallowest facies, which have the greatest benthic diversity, are eliminated from the record together with their associated faunas. The elimination of these faunas from the fossil record has the appearance of a mass extinction, but is in fact an artefact of non-preservation (Smith *et al.* 2001). Using the same argument, during a regression sedimentary facies and their associated faunas would migrate offshore, where the deepest facies would not be preserved. As graptoloid diversity is greatest near the continental margin (Finney & Berry 1997), any migration offshore would cause an apparent extinction in graptoloids. The *lundgreni* event is probably a genuine extinction event rather than an artefact, because some lineages become extinct during or shortly after the event, e.g. *Cyrtograptus*. If the event was purely an artefact of sea level change, it would be expected that only deeper-water forms would vanish, and those lineages would reappear once sea level rose again. However, this is not the case; shallow-water species such as *Testograptus testis* (see Section 2.6) become extinct. However, although the *lundgreni* event cannot be explained purely as an artefact of sea level change, the effect might make the event appear more severe than it actually was.

2.7.3 Anoxia

Both expansion (Quinby-Hunt & Berry 1991) and retreat of anoxia (Koren' 1987; Štorch 1995) have been cited as causes of graptoloid extinctions. At least some graptoloid extinctions are correlated with increased oxygenation of the sea floor, e.g. the end-Ordovician extinction (Melchin & Mitchell 1991), the *turriculatus* event (Melchin *et al.* 1998) and the Llandovery-Wenlock boundary event (Melchin 1994). At the time of the *lundgreni* event, some areas show sedimentological changes indicating oxygenation of the sea floor, for example mottled mudstones in the Welsh Basin (Warren *et al.* 1984). Oxia (loss of anoxia) has been blamed for the graptoloid extinction at the end of the Ordovician (Hallam & Wignall 1997 p.59), the mechanism being the loss of nutrients from the oceanic system, causing a decline in productivity.

Anoxic bottom conditions are seen at extinction events in some planktonic groups, for example Devonian and Carboniferous ammonoids (Becker 1993; House 1993). Anoxia has been blamed for graptoloid extinctions; Quinby-Hunt & Berry (1991) attributed graptoloid extinction at the *lundgreni* event to expansion of anoxic waters into shallower depths, which killed deeper-water graptoloids. The survivors, according to these authors, were shallow-water species; they claim that graptoloids are found in deep- and shallow-water deposits before the event, but only in shallow-water deposits after the event. The problem with this hypothesis is that some species found in shallow-water become extinct, such as *Testograptus testis* (Section 2.6). Also, it would be expected that benthic animals would be adversely affected by anoxic waters, but there is no extinction in the benthos at this time. This hypothesis is discussed further in Section 3.6.

2.7.4 Changes in nutrient supply and productivity

In modern faunas, primary productivity and diversity are linked by a known but unexplained relationship. Diversity is lowest at very low and very high productivities, and is greatest at intermediate productivities (Rosenzweig & Abramsky 1993). This is shown graphically in Figure 2.4. Nutrient levels can be used as a proxy for productivity: the higher the nutrient levels, the greater the productivity. The explanation for the lower end of the curve is straightforward; at low productivity there is a low biomass, thus a low number of individuals. Clearly there cannot be more species present in an area than there are individuals; hence a low number of individuals means a low number of species (Rosenzweig & Abramsky 1993). The reason for the low diversity at high productivity is unknown – there are many hypotheses for the pattern in the ecological literature, but as yet there is no conclusive explanation (Rosenzweig & Abramsky 1993). Valentine (1971) applied this relationship to faunas in deep time: he concluded that high diversity communities would occur in low nutrient conditions and low diversity communities in high nutrient conditions. Because nutrient supply affects diversity, extinctions could be caused by increases in nutrients.

Many of the experiments on the relationship between productivity and diversity have been conducted on small scales, both spatially and temporally. The questions of whether the relationship applies at the global scale and over geological timescales must be addressed. The relationship does appear to be valid over large spatial scales (Rosenzweig 1995 p.348), although it is not known whether it applies globally

(Rosenzweig 1995 p. 370-1). It also seems to be valid over geological timescales. Lazarus (2002) discovered that, for Neogene Antarctic radiolaria, productivity and diversity were inversely correlated, with times of increased productivity also being times of elevated extinction rates and turnover of species.

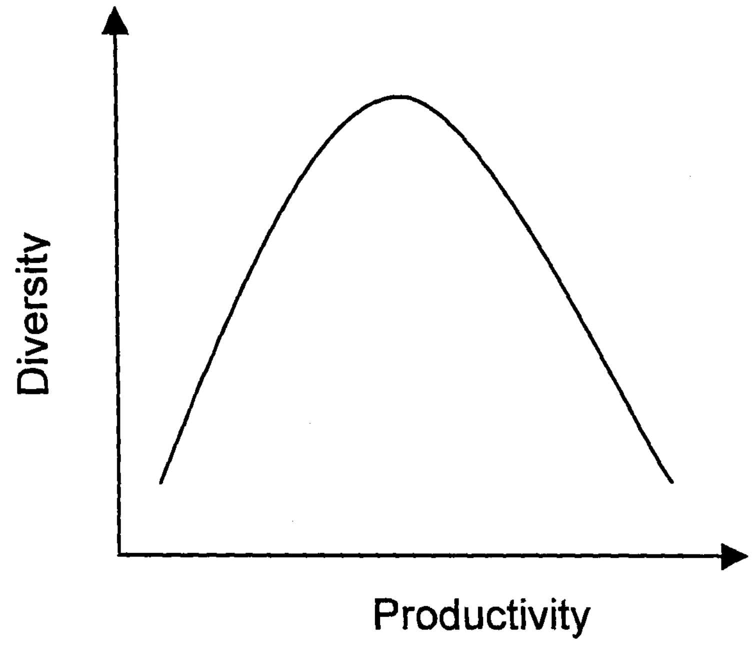


Figure 2.4: *The relationship between primary productivity and diversity. After figures in Rosenzweig (1995), schematic only.*

Several authors invoke changes in nutrient levels (and therefore in primary productivity) as an explanation for extinction events. Both increases (Hallam & Wignall 1997 p.59; Jeppsson & Calner 2003) and decreases (Valentine 1971; Hallock 1987) in productivity have been cited as a cause of extinctions. Both are theoretically possible, depending where on the productivity-diversity curve a community was originally. For very oligotrophic conditions, an increase in productivity would result in increased diversity, but for a community in the middle of the productivity axis, the same increase would cause a decrease in diversity (Figure 2.4). Hence it would be useful to know absolute values of palaeoproductivity, not just whether it has increased or decreased.

When discussing changes in palaeoproductivity as a mechanism for causing extinction, it is useful to have some measurement of it. Palaeoproductivity can be measured using a variety of techniques, including carbon isotopes (Jarvis *et al.* 2002) and barium concentrations in sediment (von Breymann *et al.* 1992). The concentration of barium is unsuitable for use as a palaeoproductivity indicator in anoxic environments and in areas where water depth has varied (von Breymann *et al.* 1992), which may limit this method's usefulness in graptolitic rocks. Carbon isotope evidence for productivity changes at the *lundgreni* event is discussed below (section 2.7.6).

2.7.5 Jeppsson model

The Jeppsson model describes oceanic conditions as an oscillation between "primo" and "secundo" states. Primo (P) episodes are those with colder high latitudes and humid low latitudes: secundo (S) episodes have dry low latitudes and warm high latitudes (Jeppsson 1990; Jeppsson *et al.* 1993). Table 2.18 compares some characteristics of P and S episodes. The model predicts low planktic diversities during secundo episodes (times of lower sea level) and high diversity during primo episodes (higher sea level). The mechanism for this is increased nutrient levels from upwelling and enhanced continental weathering during primo episodes, leading to increased primary productivity and increased plankton abundance. Secundo episodes have lower nutrient levels, so very reduced primary productivity (perhaps only ten percent of that during primo episodes), hence a lowered abundance and diversity of plankton (Jeppsson 1990). S and P episodes have so far been identified for the Llandovery (Aldridge *et al.* 1993), Wenlock (Jeppsson *et al.* 1995) and Ludlow (Jeppsson & Aldridge 2000). Extinctions can occur during transitions from P to S, S to P, S to S or P to P states, although this is less likely for P-P events than for the other possibilities (Jeppsson 1998). A list of graptoloid extinctions and the events correlated with them is given in Table 2.19. The *lundgreni* event is correlated with the Mulde Secundo-Secundo Event (Jeppsson *et al.* 1995; Jeppsson & Calner 2003), with the graptoloid extinctions being due to a fall in planktic productivity (Jeppsson & Calner 2003).

The Jeppsson model has been criticised (Loydell 1994, 1998; Melchin *et al.* 1998) on the grounds that not all events are correlated with graptoloid extinctions, for example an event (the Valleviken Event of Jeppsson *et al.* 1995) is identified in the *lundgreni* Zone, but there is no graptoloid extinction during that zone (Melchin *et al.* 1998). Also, the model assumes that plankton diversity is directly correlated with nutrient levels, with an increase in nutrient levels leading to an increase in diversity, but this is not the case, except at very low levels of nutrients (Section 2.7.4). Furthermore, the model does not appear to fit the pattern seen in the Welsh Basin, where graptolite diversity falls at the time of oxic bottom waters (the *lundgreni* event is correlated with oxic conditions in North Wales (Warren *et al.* 1984) and the Long Mountain (Palmer 1972)). This is the opposite effect from that predicted by the primo-secundo model.

Table 2.18: *Some characteristics of primo and secundo episodes, from Jeppsson (1990).*

	Primo	**Secundo**
Sea level	Higher	Lower
Carbonates	Argillaceous	Pure
Deep water	Oxic	Anoxic
Benthic productivity	Low	High
Planktic productivity	High	Low
Plankton	Abundant and diverse	Sparse and not diverse
Most important nutrient sources	Upwelling and continental weathering	Benthic recycling
Weathering rate	High	Low

Table 2.19: *Correlation of graptoloid extinction events with the oceanic events of the Jeppsson model.*

Extinction event	**Correlated with**	**Reference**
bouceki-transgrediens	Klonk Secundo-Unnamed Event	Jeppsson 1998
formosus	Klev S-P event	Jeppsson 1998; Jeppsson & Aldridge 2000
bohemicus tenuis-kozlowskii	Lau Event	Jeppsson 1998; Jeppsson & Aldridge 2000
leintwardinensis	Linde P-S Event	Jeppsson 1998; Jeppsson & Aldridge 2000
lundgreni	beginning of Mulde Event	Melchin *et al.* 1998
centrifugus-murchisoni	Ireviken Event (latest part)	Melchin *et al.* 1998
lapworthi-insectus	Ireviken Event (earliest part)	Melchin *et al.* 1998
turriculatus-crispus	unnamed secundo-primo event	Jeppsson 1996
sedgwickii	Sandvika Event	Melchin *et al.* 1998

2.7.6 Geochemical evidence

Strontium isotope curves for the Silurian (Azmy *et al.* 1999; Ruppel *et al.* 1996) show an increase in $^{87}Sr/^{86}Sr$ during the Homerian. (Correlation of the conodont biozones used by Ruppel *et al.* with the graptoloid biozones follows Saltzman (2001), who correlates the top of the *lundgreni* to the *ludensis* zones with the early part of the *crassa* conodont Biozone.) Azmy *et al.* (1999) attributed the increase in $^{87}Sr/^{86}Sr$ values through the Silurian to an increase in continental weathering, so the increase during the Homerian also reflects this. This increase in weathering probably resulted in an increased nutrient supply to the oceans.

The ratio of carbon-12 to carbon-13 in the oceans depends upon biological productivity, because photosynthesising organisms preferentially take up carbon-12. Thus an increase in biological productivity leads to an increase in the relative proportion of carbon-13 in the oceans. In the geological record, a positive $\delta^{13}C$

excursion (i.e. removal of carbon-12 from the ocean) indicates an increase in primary productivity and/or increased burial of organic matter (Jarvis *et al.* 2002; Schlanger *et al.* 1987).

There is general agreement that there is a positive $\delta^{13}C$ excursion during the *parvus-nassa* Zone (Corfield & Siveter 1992; Corfield *et al.* 1992; Kaljo *et al.* 1997; Kaljo *et al.* 1998; Saltzmann 2001). (All the references listed are from Baltica, Laurentia or Avalonia, which were all close together at this time. Thus these results may only be representative of this area, and there may have been different patterns in other places.) This positive excursion could represent an increase in primary productivity, an increase in the amount of organic matter buried, or both. If there were an increase in the amount of organic matter buried, then there should be an increase in the amount of organic matter seen in the sedimentary record (e.g. an increase in the amount of black shale deposition). However, as discussed below (Section 2.8), there is no consistent change in sediment type at the end of the *lundgreni* Zone. The "Grenzkohlenfluchen" (boundary coal seam) of Jaeger (1991) probably represents an increase in organic matter burial, but other areas do not have similar deposits. Thus it does not appear that there is a significant increase in organic matter burial, and therefore the positive $\delta^{13}C$ excursion is due to an increase in productivity.

Some authors (Kaljo *et al.* 1997; Kaljo *et al.* 1998) have found a $\delta^{13}C$ depletion at the top of the *lundgreni* Zone, which could imply a decrease in productivity (Hallam & Wignall 1997 p.21). However, this has only been detected in studies from the Baltic region, and so may reflect local rather than global conditions.

2.8 Sedimentological changes at the end of the *lundgreni* Zone

As changes in the environment are likely to cause changes in the nature of deposited sediment, changes in sediment type or characteristics give valuable information about the environment at the time of deposition. Thus sedimentological studies can be extremely useful when testing hypothesis of extinction causes, especially the hypotheses that the extinction was caused by an expansion (Quinby-Hunt & Berry 1991) or by a retreat of anoxia (Koren' 1987; Štorch 1995). Unfortunately there is little information in the literature – even where sedimentary logs are given on a graptolite range chart, there is rarely interpretation of the environment of deposition. This makes it difficult to assess the nature and extent of sedimentological changes at this time.

Changes are seen in some areas at the end of the *lundgreni* Zone, but not in others. In the Welsh Basin, there is a change from anoxic to oxic sediments late in the *lundgreni* Zone (Warren *et al.* 1984; Chapter 3 of this thesis). Changes are seen at or near the end of the *lundgreni* Zone in Germany (Jaeger 1991, a "Grenzkohlenfluchen" (boundary coal seam)), Sweden (Laufield *et al.* 1975, a change from dark grey shale to olive-grey mudstone at the beginning of the *ludensis* Zone *s.l.*) and Morocco (Destombes *et al.* 1984 p. 243, a change from clay with limestone lenses to ferruginous limestone). In central Asia, sediment type changes from mudstone to turbiditic sandstone at the end of the *lundgreni* Zone in some sections, (Koren' & Suyarkova 1994 Figure 3) but this may not be meaningful, as turbiditic sandstones appear in other sections in the middle of zones (Koren' & Suyarkova 1994 Figure 4). Volcanic ashes are found at the end of the *lundgreni* Zone in Spain (Gutierrez-Marco *et al.* 1996). The only one of these deposits that obviously represents an increase in the amount of organic carbon being buried is the "Grenzkohlenfluchen" of Jaeger (1991) (see Section 2.7).

There appears to be no change in sedimentology in Poland, Arctic Canada (Kozłowska-Dawidziuk *et al.* 2001) and Nevada (Berry & Murphy 1975). In Latvia, Ulst (1974) reported a reduction in the clay content of one section. Otherwise there are apparently minor sedimentological changes in the Baltic region (Kozłowska-Dawidziuk *et al.* 2001).

Thus there is no consistent change globally. This may partly reflect differing water depths – shallower-water sections would be expected to be affected more than deeper sections by sea-level change. Where lithological changes are seen, the beds are thin with respect to the thickness of the *lundgreni* Zone. This implies that the extinction event was short-lived (on a geological timescale), although exact durations cannot be determined.

2.9 Summary

Graptoloid diversity during the Silurian shows an overall decline, with peaks during the Llandovery, Wenlock, early Ludlow and Přídolí. Many extinction events occurred, of which the late Wenlock *lundgreni* event is one of the most significant. The survivors of extinction events tend to be small species with a simple morphology (e.g. pristiograptids). The *lundgreni* event follows this pattern, with the widespread surviving species (*Pristiograptus dubius*, *Pristiograptus parvus* and *Gothograptus nassa*) being small and morphologically simple.

The *lundgreni* event was one of the most severe of the Early Silurian in terms of percentage extinction, termination of lineages and subsequent low diversity. The event has been seen in some other planktonic groups, but does not appear to have affected the benthos. During the succeeding *parvus-nassa* Zone, global diversity is approximately ten species, but the diversity seen in any individual section is much lower. Mass occurrences of *Pristiograptus parvus* and *Gothograptus nassa* are found in some areas. In the *praedeubeli-deubeli* and *ludensis s.s.* zones diversity recovers, with the radiation of the *Colonograptus ludensis* group, the *Lobograptus? sherrardae* group and retiolitids. *Cyrtograptus*, *Testograptus* and hooked monograptids become extinct during the event in most of the world, but appear to survive in a few areas, mostly Australia.

It has been suggested that that deeper-water species became extinct during the *lundgreni* event, with shallow-water species surviving. A review of depth zonation using available evidence from the Welsh Basin and Arctic Canada does not support this, as some shallow-water species become extinct, e.g. *Testograptus testis,* *Cyrtograptus* and *Monograptus flemingii*, and some survivors are found in deeper water, such as *Pristiograptus dubius*.

Bolide impact, sea level changes, expansion of anoxia, retreat of anoxia and changes in primary productivity have all been suggested as causes of the *lundgreni* event. There is no evidence to support a bolide impact. The event occurs at the same time as a regression, as do many other graptoloid extinction events. However, sea level fall is thought to be correlated with some factor that causes extinction rather than being the direct cause of extinction events. Sea level change may have made the event appear more severe than it actually was, because of taphonomic effects.

At least some graptoloid extinctions are correlated with increased oxygenation of the sea floor. Although there are environmental changes indicating a shift from anoxic to oxygenated conditions at the end of the *lundgreni* Zone in the Welsh Basin, there is no consistent environmental change globally. Some areas do not appear to show any change at all.

Some workers have attributed extinction events to a change in primary productivity, either an increase (Jeppsson's primo-secundo model) or a decrease (e.g. Valentine 1971). In modern systems, increased productivity is correlated with decreased diversity (except at very low productivities), although the reasons for this are unclear. There was a positive $\delta^{13}C$ excursion during the *parvus-nassa* Zone, which was probably caused by an increase in primary productivity. This does not agree with the Jeppsson model, which predicts a fall in primary productivity at this time (Jeppsson & Calner 2003), but is in agreement with other models that correlate increases in primary productivity with decreases in diversity. The increase in nutrients may have resulted from an increase in continental runoff, because of a greater continental area exposed during the regression that occurred in most areas at the end of the *lundgreni* Zone.

3. Fieldwork in the Welsh Borderland

3.1 Introduction and geological background

The Long Mountain is situated on the Anglo-Welsh border between Shrewsbury and Welshpool (Figure 3.1). During the Silurian the area was situated on the palaeoslope of the Welsh Basin, between the shallow water of the Midland Platform in the present-day Midlands and deeper water in North Wales (Aldridge *et al.* 2001). The area was mapped in detail and formations defined by Palmer (1969, 1972). The rocks of the Long Mountain form an asymmetrical syncline exposing Llandovery to Přídolí strata (Palmer 1972; Aldridge *et al.* 2001). The Llandovery and Wenlock rocks consist of graptolitic mudstones, sometimes laminated, with occasional shelly bands (Palmer 1972). Deposition appears to have been more or less continuous from the upper Llandovery to the upper Wenlock (Palmer 1972). During the Ludlow, deposits were more varied, with graptolitic siltstones, turbiditic siltstones and shelly slumped beds occurring in different parts of the area, depositional style apparently being controlled by bottom topography (Palmer 1972). By the middle Ludlow (*leintwardinensis* Zone) siltstones with a mixed graptolitic and shelly fauna were being deposited over the whole area (Palmer 1972). The rocks above this are non-graptolitic and will not be discussed here. The Long Mountain rocks have been divided into various formations on the basis of their graptolite faunas (Palmer 1969, 1972), of which the one of greatest interest here is the Trewern Brook Mudstone Formation (TBMF) of Palmer (1969). The TBMF includes the *centrifugus-murchisoni* to *lundgreni* biozones, and includes at its top the Glyn Member, a calcareous shelly mudstone of variable thickness (Palmer 1969, 1972). The Glyn Member is of particular significance because it occurs at the top of the *lundgreni* Zone. This is discussed in more detail below (section 3.6). The TBMF is succeeded by the Long Mountain Siltstone Formation, which covers the *nilssoni* to *bohemicus* biozones (Palmer 1972).

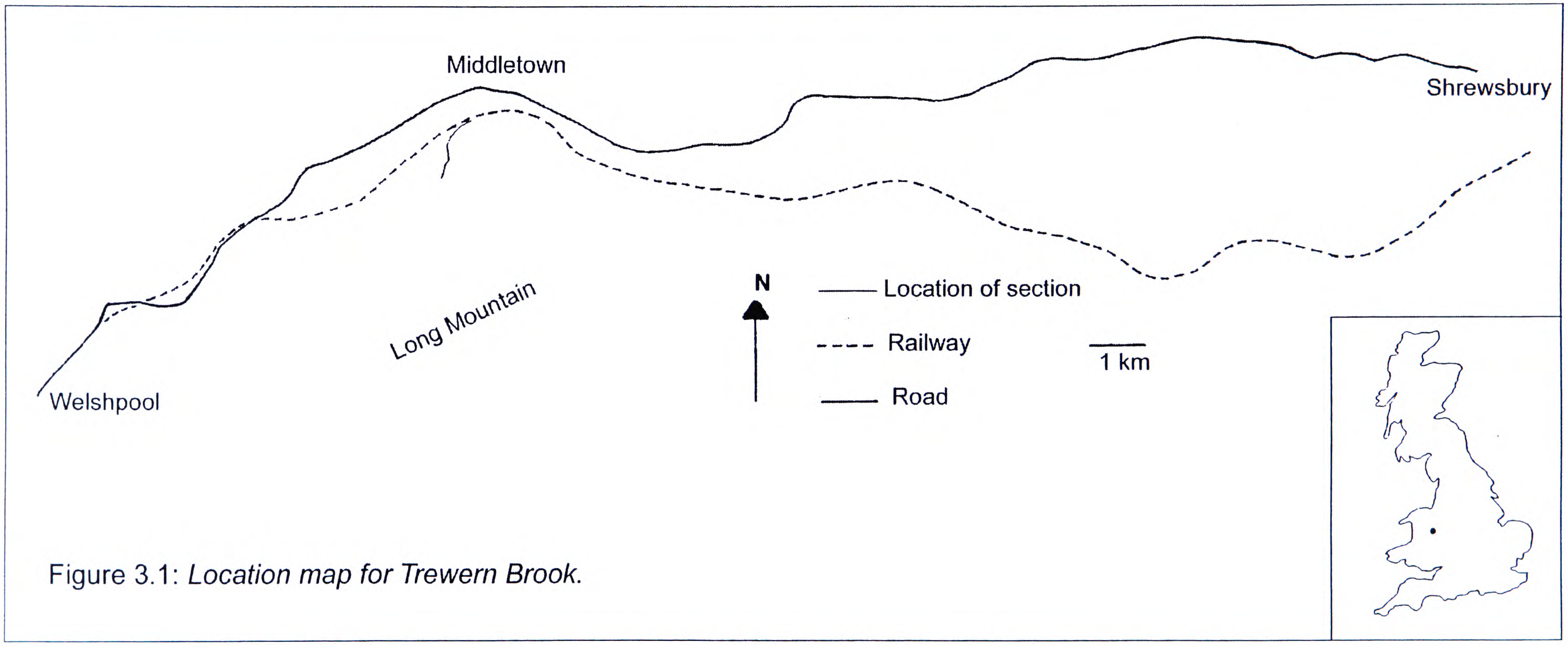


Figure 3.1: *Location map for Trewern Brook.*

The graptoloids of the Long Mountain have been studied by Elles (1900), Wood (1900), Das Gupta (1932, 1933), Palmer (1972), Holland & Palmer (1974) and Rickards & Palmer (2002). Graptolite zones from the upper Llandovery to the *bohemicus* Zone (Ludlow) are seen (Palmer 1969; Holland & Palmer 1974; Aldridge *et al.* 2001). For a comprehensive historical review of geological studies in the area, see Palmer (1972).

The Long Mountain was chosen as a study area because of the lack of tectonic deformation of the graptoloids, because the graptoloid faunas and zones had already been described in detail (Palmer 1972), and because the faunas had not been worked on for thirty years. Graptoloids were collected from a section along Trewern Brook on the north side of the Long Mountain (grid reference SJ 3305 3115). This section is the only one in the area to show a complete section through the *lundgreni* Zone (Palmer 1972). In this section the TBMF covers the *lundgreni* Zone, the Glyn Member the *nassa-dubius* and the base of the *ludensis s.l.* zones, and the Long Mountain Siltstone Formation the *ludensis* Zone *s.l.* upwards, with the exact boundary between the *lundgreni* and *nassa-dubius* zones unclear (Palmer 1972). The section is a geological Site of Special Scientific Interest and the type section of the Trewern Brook Mudstone Formation (Palmer 1969). As the stream marks the border between England and Wales, the site falls within the jurisdiction of both English Nature and the Countryside Commission for Wales. The aims of the fieldwork were to see whether or not there were environmental changes at the time of the *lundgreni* extinction, to see whether the extinction was sudden or gradual and to study the faunas using statistical techniques such as rarefaction and capture-recapture. This chapter is based on three weeks of fieldwork in July 2000. No fieldwork was done in 2001, because foot and mouth disease made access to the land impossible. Instead the collections of Palmer (1972) and Elles (1900) from Trewern Brook were examined.

3.2 Description of section and collecting methods

The TBMF is a blue-grey mudstone, sometimes calcareous, with occasional nodular horizons. Some beds contain laminations whereas others are more massive. The formation contains many bands of white clay, interpreted as volcanic ashes, in some parts of the section as frequently as one every metre. Exposure is generally reasonable along the studied section, although some localities were entirely underwater and could only be found by wading. For this study fossils were collected from the upper part of the *lundgreni* Zone, the *nassa* Zone and part of the *ludensis* Zone *s.l.* (The *praedeubeli-deubeli* and *ludensis s.s.* zones have not yet been recognised in Britain.)

Figure 3.2 gives locality and strike and dip information for the studied section. Several samples from different beds were collected at some localities (four samples at Locality 20, two at Locality 22 and two at Locality 24). Detailed locality information is deposited with the collection in Edinburgh University. A fault at Locality 8, a small quarry, is marked by a change in strike (Figure 3.2). A change in strike is also present in the stream between localities 27 and 29. (It was not possible to measure dip and strike at localities 28 and 34). This change in strike may mark the continuation of the fault at Locality 8, or may reflect small folds in the area (marked on the map of Palmer 1972).

Fossils are not common – the abundances listed for most of the localities below represent approximately half a day's collecting. Samples were collected at intervals up the section. The thicknesses of rock between the localities were worked out, using trigonometry, from measurements of distances, dips and bearings taken in the field. Collecting was begun south of the railway line because there is a fault near where the railway line crosses the stream (Palmer 1972). All fossils observed, not just the graptolites, were collected.

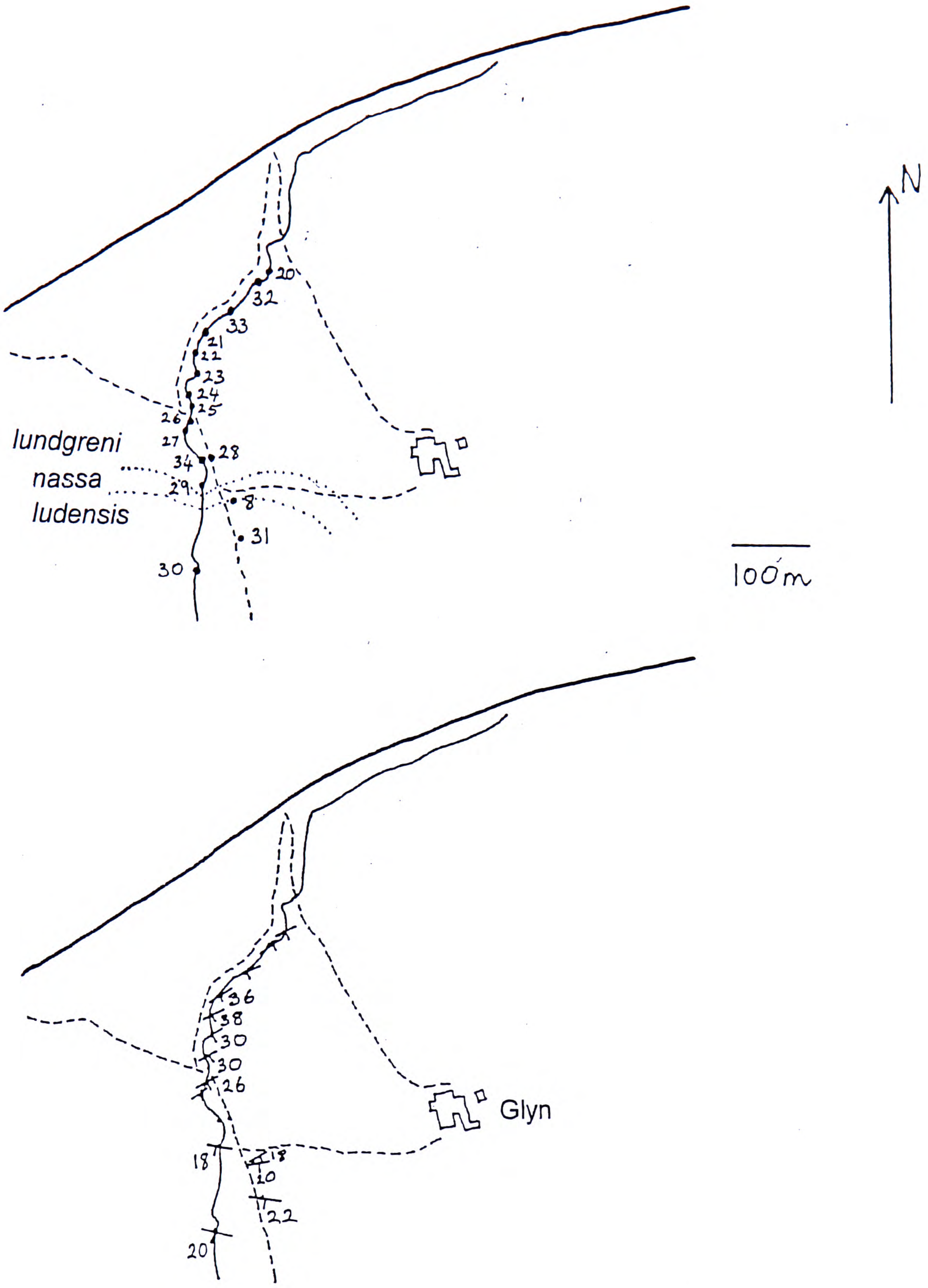


Figure 3.2: *Localities and strikes and dips for the Trewern Brook section. Stream flows and rocks young southwards. All localities are in the Trewern Brook Mudstone Formation. Zonal boundaries are from the map of Palmer (1972), with the position of the* nassa-ludensis *boundary slightly revised to take account of Locality 8 being of* ludensis *Zone age.*

———	Stream	☐	Building
- - - - -	Path/road	•	Locality
━━━	Railway line	⊤ 30	Strike, dip and dip direction
………..	Biozone boundary		

The graptoloids are preserved in relief or partial relief, and some are partially or wholly pyritised. The periderm is preserved as a black film, except in specimens where the graptoloid has been weathered out leaving an external mould. Preservation on unweathered surfaces is extremely good.

3.3 Results

The graptoloids found in the section are shown graphically in Figure 3.3, and illustrated in Figure 3.4. In the lower part of the sequence (localities 20 to 27), the fauna consists of *Monograptus flemingii, Pristiograptus dubius, Pristiograptus parvus, Monoclimacis flumendosae, Cyrtograptus* sp. or spp., *Pristiograptus* cf. *Pristiograptus* sp. 1 Holland, Rickards & Warren 1969 and nautiloids. Burrows appear at Locality 26 and persist thereafter. At localities 28 and 34 no graptoloids were found. This level contains an abundant shelly fauna with many burrows, identified as the Glyn Member of Palmer (1969, 1972). Locality 29 contains abundant *Gothograptus nassa*, but no other graptoloids were found. At Locality 8 there is a return to the graptolite-nautiloid assemblage with occasional bivalves (*Cardiola* sp.) and abundant pyritised burrows. Above this, at localities 31 and 30, an assemblage of brachiopods, trilobites, ostracodes and occasional graptoloids is found. The graptoloids here are mostly fragments of indeterminate pristiograptids, but some can be recognised as *Pristiograptus dubius.*

The *lundgreni* Zone is recognised by the presence of cyrtograptids, *Monograptus flemingii* and *Monoclimacis flumendosae*. The base of the *nassa* Zone is marked by the first appearance of *Gothograptus nassa*. The non-graptolitic interval cannot be assigned to either the *lundgreni* Zone or the *nassa* Zone, as no graptoloids have been found in that part of the sequence. The base of the *ludensis* Zone is drawn at the first appearance of *Colonograptus ludensis*.

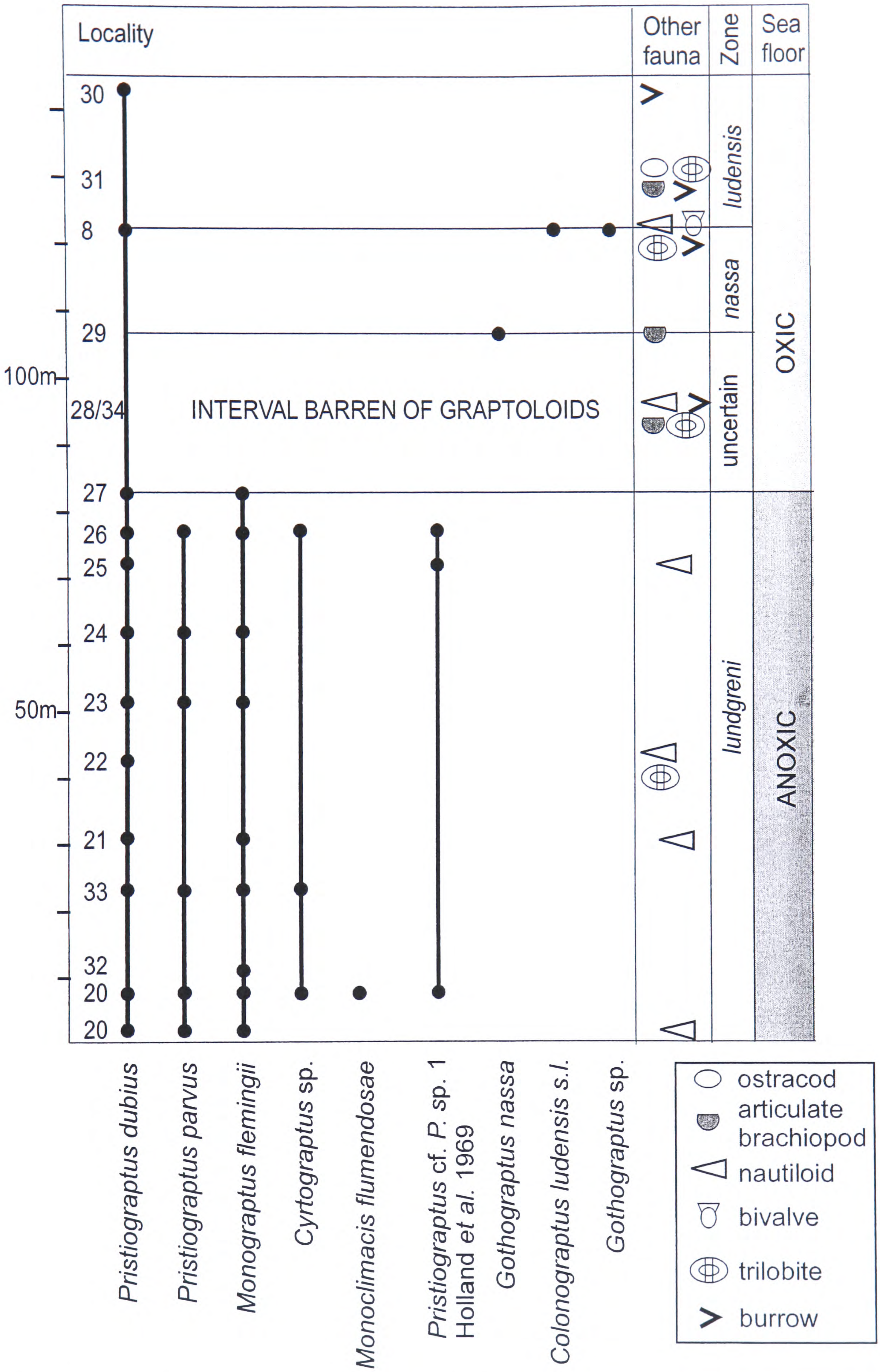


Figure 3.3: *Range chart of the graptoloids of the Trewern Brook section.*

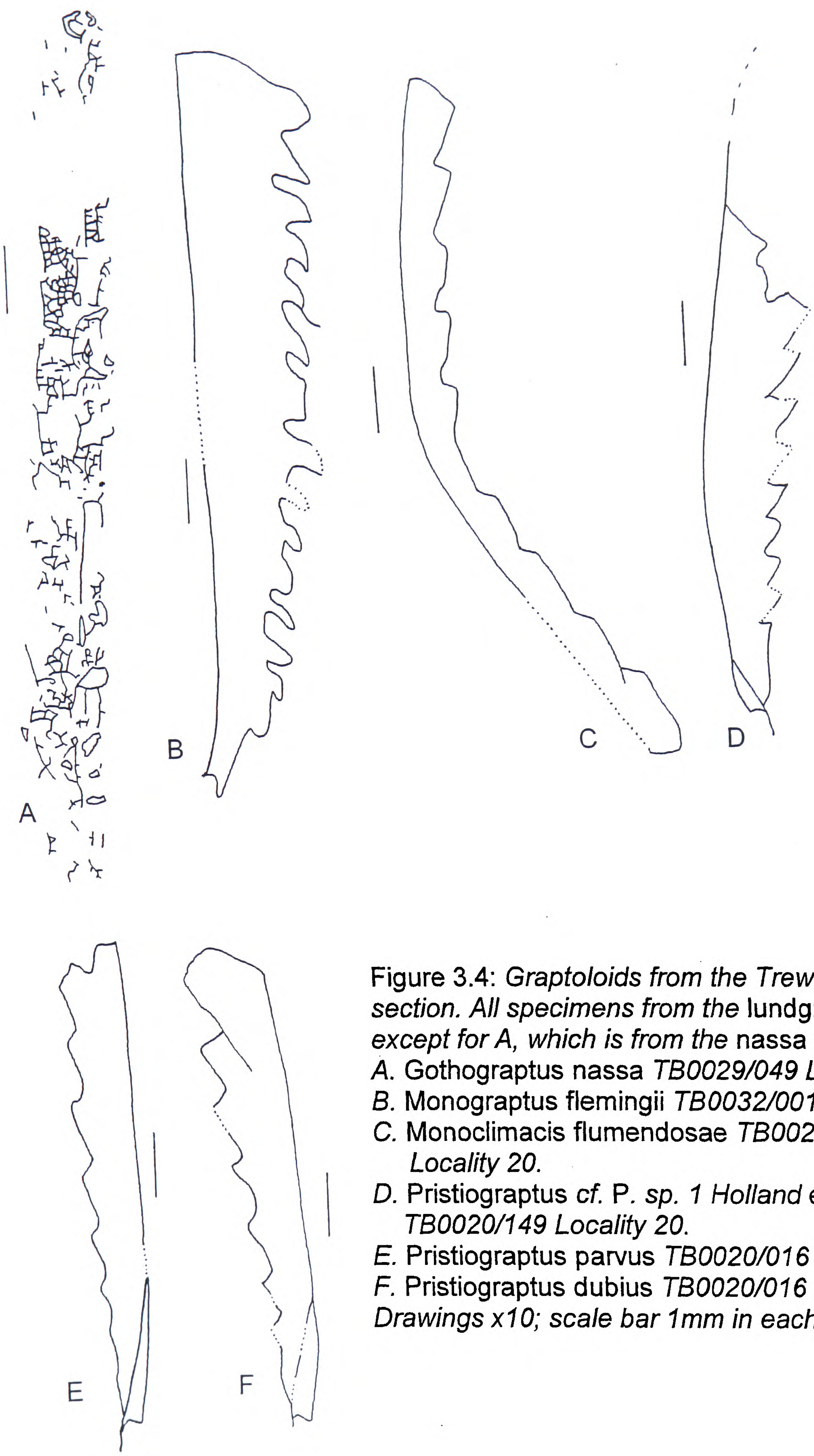


Figure 3.4: *Graptoloids from the Trewern Brook section. All specimens from the* lundgreni *Zone except for A, which is from the* nassa *Zone.*

A. Gothograptus nassa *TB0029/049 Locality 29.*

B. Monograptus flemingii *TB0032/001 Locality 20.*

C. Monoclimacis flumendosae *TB0020/134 Locality 20.*

D. Pristiograptus *cf.* P. *sp. 1 Holland* et al. *1969 TB0020/149 Locality 20.*

E. Pristiograptus parvus *TB0020/016 Locality 20.*

F. Pristiograptus dubius *TB0020/016 Locality 20.*

Drawings x10; scale bar 1mm in each case.

3.4 Numerical studies

The number of specimens of each species at each locality is given in Table 3.1, and plotted as a percentage of the total number of specimens at each locality in Figure 3.5. Figure 3.6 shows the total number of specimens of each species found in the *lundgreni* Zone. *Monograptus flemingii* and *Pristiograptus dubius* dominate the assemblages, with cyrtograptids and *Monoclimacis flumendosae* being rarer. This was also noted by Elles (1900, Table III), who stated that *M. flemingii* and *P. dubius* were "very common" throughout the zone and cytograptids "very rare".

The relative abundances of species appear to change through the *lundgreni* Zone; in particular, *Monograptus flemingii* appears to become less common relative to other species towards the end of the zone (Figure 3.5). Nothing can be said about graptoloid abundances in absolute terms. It is possible that the absolute abundance of *M. flemingii* in fact increased up the section, if absolute abundances of all the other graptoloids also increased.

The question of adequacy of sampling is one that must be addressed. Are the results given here a good approximation to reality, or could they be artefacts of inadequate sampling? In an area where graptoloids are more abundant, it would have been possible to adopt a collecting strategy where collecting continues until a set number of specimens are found. (Obviously when using this strategy there can be no selection of specimens – all specimens found up to the desired number must be kept, or the sample will be biased.) This would have allowed a direct comparison of the proportions of different species between localities. However, the rarity of graptolites in this area did not allow this.

Collector bias is unlikely to have significantly affected this study with respect to the monograptids, because all fossils seen in the field were collected. For retiolitids it will have been a problem – retiolitid fragments invisible to the naked eye were noticed under a microscope in the laboratory. Almost certainly, other retiolitids were left behind on the outcrop. The exception to this is *Gothograptus nassa*, the thecal hoods of which make it visible in the field.

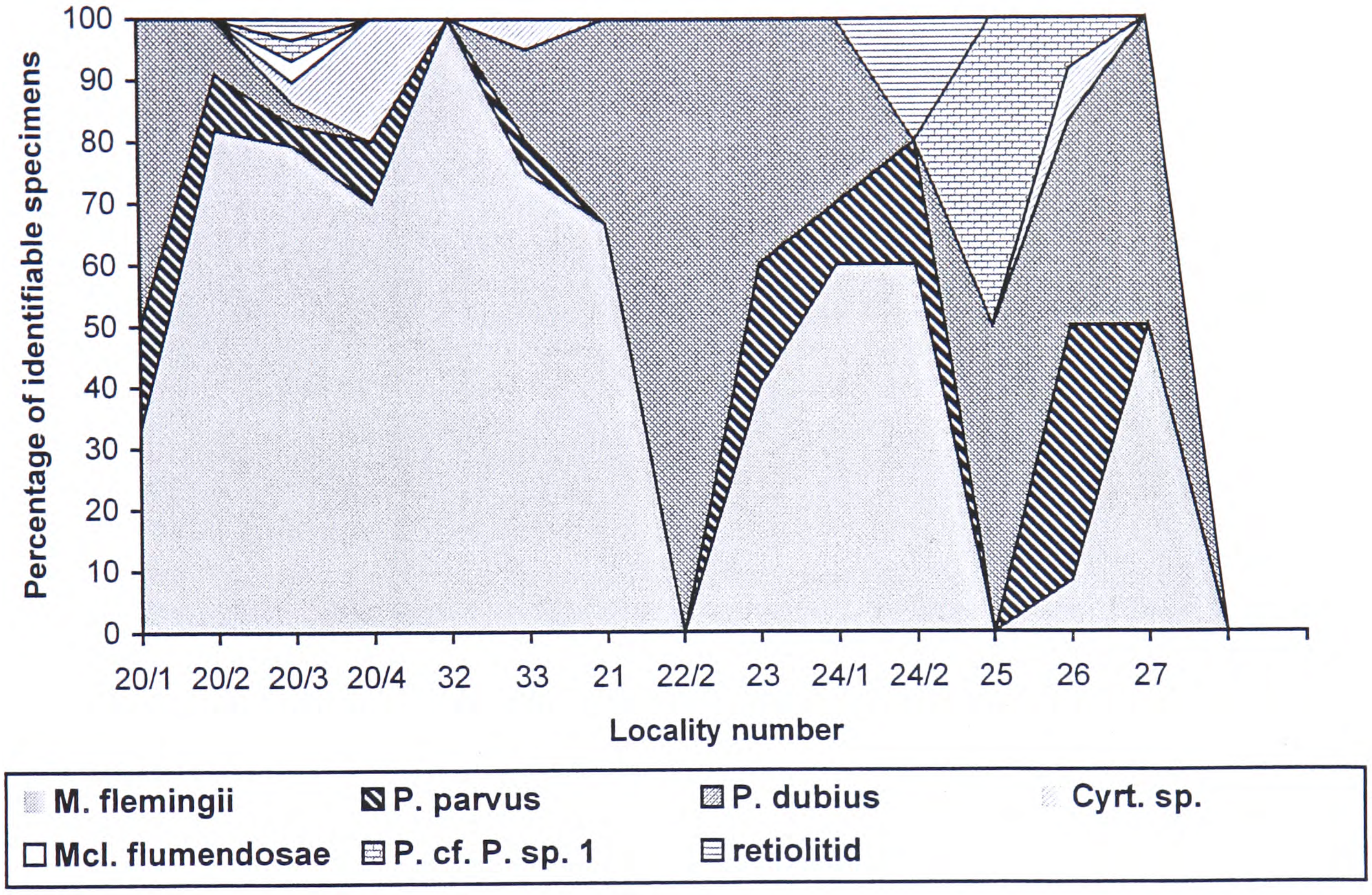


Figure 3.5: *Abundance diagram for the different species found in the* lundgreni *Zone of Trewern Brook.* M. = Monograptus, P. = Pristiograptus, Cyrt. = Cyrtograptus, Mcl. = Monoclimacis.

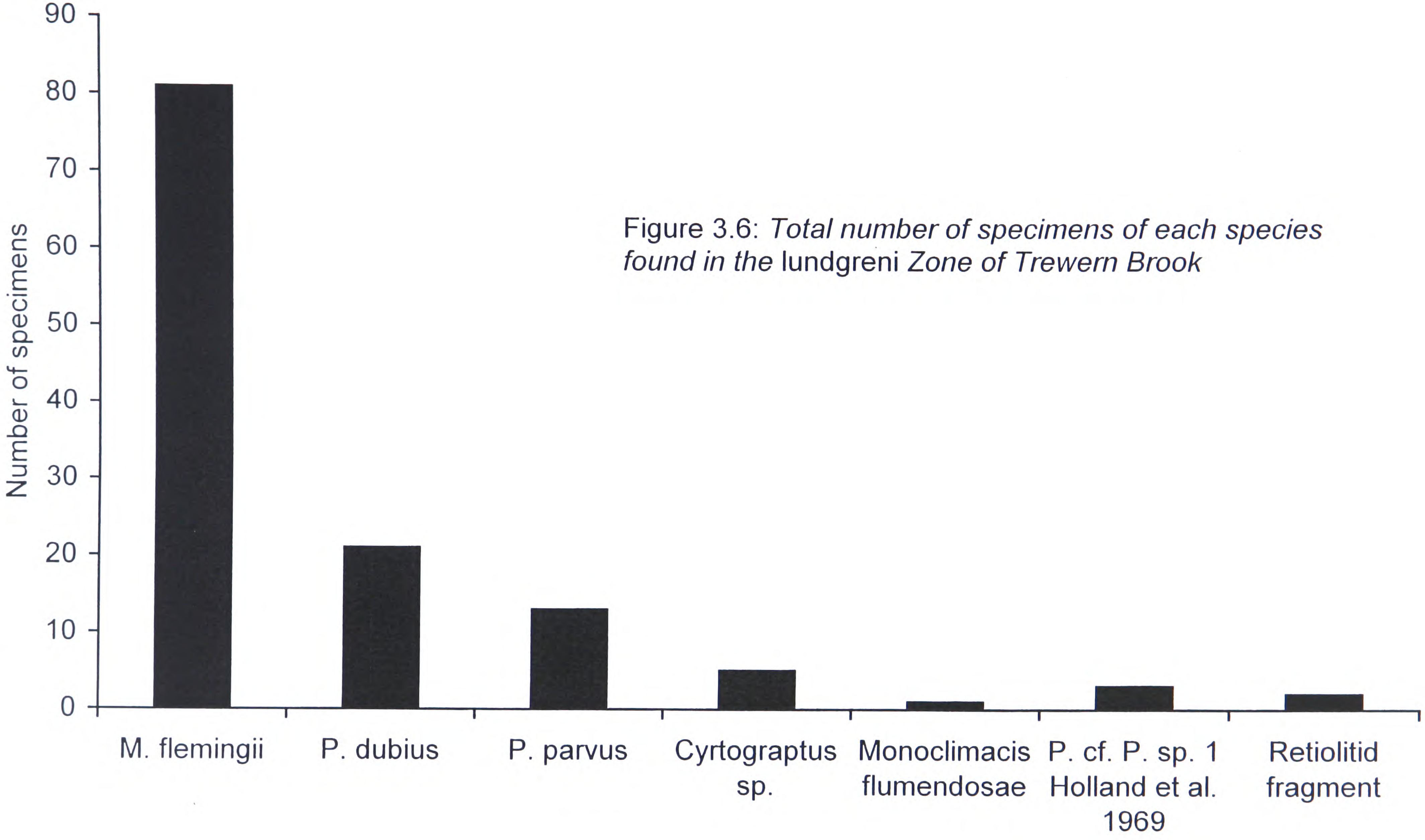


Figure 3.6: *Total number of specimens of each species found in the* lundgreni *Zone of Trewern Brook*

Table 3.1: *Number of specimens of each taxon identified at each locality for the* lundgreni *Zone of Trewern Brook.*

Locality/ sample	**Distance above base of section/ metres**	**Total identifiable specimens**	**No. of taxa identified**	***Monograptus flemingii***	***Pristiograptus parvus***	***Pristiograptus dubius***	***Cyrtograptus* sp.**	***Monoclimacis flumendosae***	***Pristiograptus* cf. *P.* sp. 1 Holland *et al.* 1969**	**Retiolitid fragment**
27	82.6	2	2	1		1				
26	76.7	12	5	1	5	4	1		1	
25	71.1	2	2	0		1			1	
24/2	62.0	5	3	3	1					1
24/1	61.0	10	3	6	1	3				
23	50.8	5	3	2	1	2				
22/2	42.3	1	1	0		1				
22/1	41.4	0	0	0						
21	30.6	3	2	2		1				
33	22.4	20	4	15	1	3	1			
32	10.8	10	1	10						
20/4	9.2	10	3	7	1		2			
20/3	7.5	29	7	23	1	1	1	1	1	1
20/2	2.9	11	3	9	1	1				
20/1	0.0	6	3	2	1	3				
Total		**126**		**81**	**13**	**21**	**5**	**1**	**3**	**2**

Sample sizes for some localities are small (see Table 3.1), as few as two specimens in some cases. This is a problem; if a sample consists of only two specimens clearly no more than two species can be present in it. The number of species recognised in a sample is positively correlated with the number of specimens in that sample. Figure 3.7 shows this graphically. This means that the number of species found will partly depend upon the size of the sample. Small samples will include only a few species, larger ones will contain more. This problem could have been partially alleviated had another season of field work been possible. Resampling of localities would not only have given larger samples, but would have made possible the use of capture-recapture methods.

Capture-recapture models are used to estimate population size from a series of random samples. In a study of an animal population, all animals caught are marked, and the numbers of marked and unmarked animals recorded for each sample. The proportion of marked to unmarked animals gives an estimate of population size (Begon *et al.* 1996 p.146). When applied to palaeontological data, the numbers of species rather than the numbers of animals are used. There are a variety of capture-recapture models available, which fall into two categories (Nichols and Pollock 1983). Closed population models assume that no births, deaths or migrations occur: open population models allow births, deaths and migration (Nichols & Pollock 1983). Pollock (1982) described a design that includes both closed and open population models. Pollock's method, as applied to palaeontology, involves sampling several beds within a sequence, taking several samples within each bed. As each bed represents a single age, it can be assumed that no speciation or extinction has taken place. Thus a closed population model is used to estimate population size (number of species present) for each bed, using the data from the multiple samples within each bed. An open population model is used on the samples from successive beds to estimate speciation, extinction and survival rates.

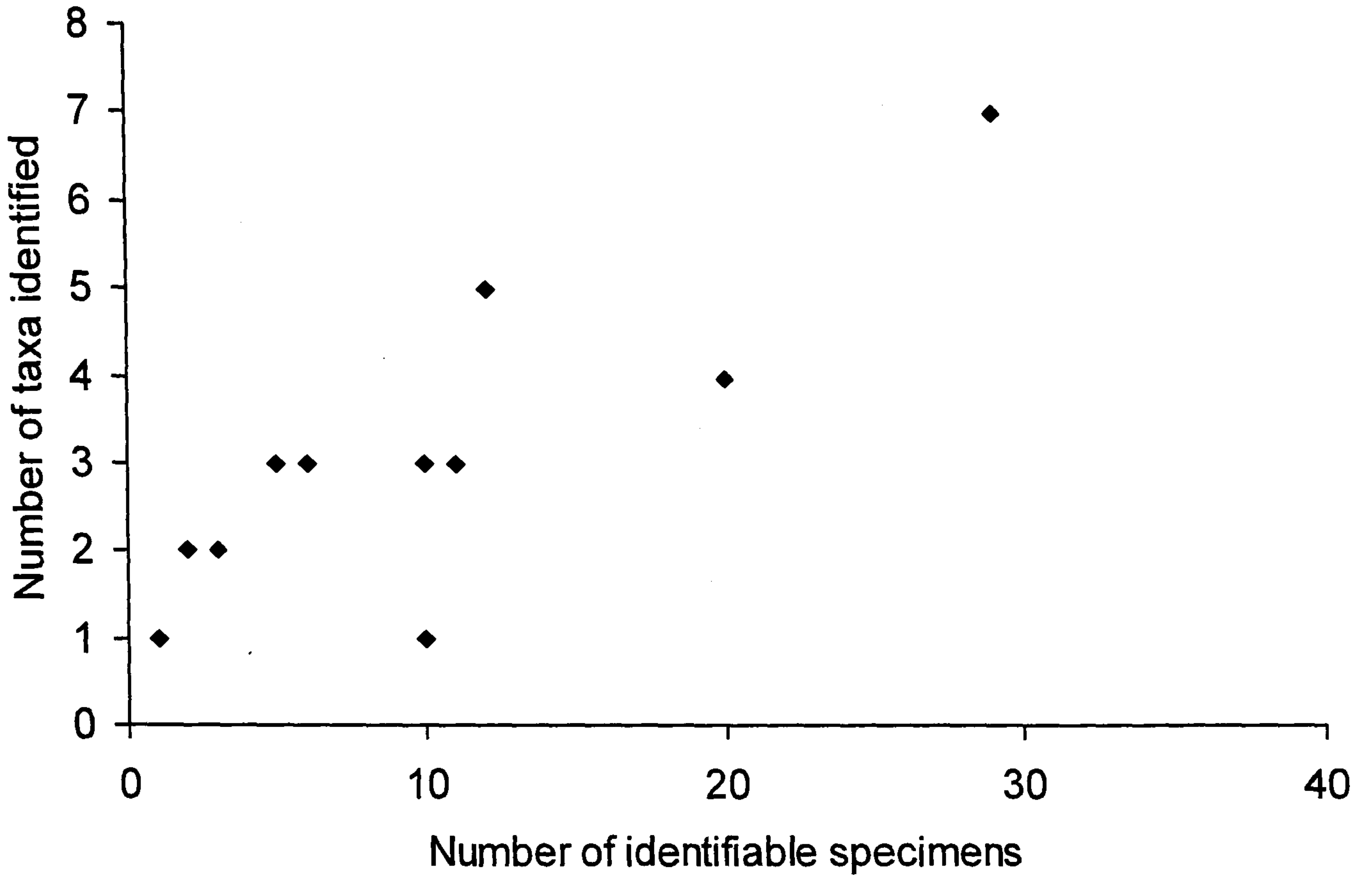


Figure 3.7: *Plot showing the correlation of the number of taxa identified with the number of identifiable specimens for the* lundgreni *Zone of the Trewern Brook section.*

3.5 Elles and Palmer collections

As no fieldwork was possible during 2001, the collections of Elles (1900) and Palmer (1972) were examined. It was hoped that the material would be appropriate to conduct statistical studies on, but this proved not to be the case.

The preserved collection of Elles (1900) in the Sedgwick Museum, Cambridge represents a small fraction of the material she must have collected. She lists *Monograptus flemingii*, *M. irfonensis*, *Pristiograptus dubius*, *Cyrtograptus lundgreni*, *Monoclimacis vomerinus* and *Testograptus testis* as occurring in the *lundgreni* Zone of the Trewern Brook section. No graptoloids from the *lundgreni* Zone of Trewern Brook were found in the collection. Thus it appears that much of the material must have not been deposited in the museum, and so it is impossible to verify Elles' identifications.

The collection of Palmer (1972) is held in the National Museum and Gallery of Wales, Cardiff. All the specimens have locality numbers scratched on them, but unfortunately there is no locality information with the collection, and Douglas Palmer no longer has his original notes (D. Palmer *pers. comm.* 2002). Some localities are mentioned in the thesis (Palmer 1972), but not all. Locality 60 is Trewern Brook (Palmer 1972), so all the graptoloids labelled as this locality were examined. The collection does not seem to be unbiased – all the specimens had proximal ends, so it appears that only the best specimens were kept. As some species are more fragile than others, and hence are less likely to be represented, this is an obvious bias, and makes the collection unsuitable for statistical study.

Some of the data gathered from this study of the Palmer collection is shown below (Figure 3.8). The localities are shown in stratigraphic order, but exact vertical thicknesses are not shown, as it was not possible to determine these. In the *lundgreni* Zone the pattern is the same as that seen in this study, with *Monograptus flemingii* and *Pristiograptus dubius* being the most common species, appearing at all or almost all the localities, and other species being rarer. The diversity in the *nassa* Zone is higher than that seen in this study, with four species present as opposed to one in this work.

3.6 Interpretation of results and conclusions

The *lundgreni* Zone fauna consists of six taxa, five of which persist until the base of the non-graptolitic interval. The fauna apparently disappears in a stepwise fashion. However, as the sample immediately below the non-graptolitic sequence consists of only two identifiable specimens, this apparent gradual disappearance is probably due to inadequate sampling and/or the Signor-Lipps effect (Signor & Lipps 1982).

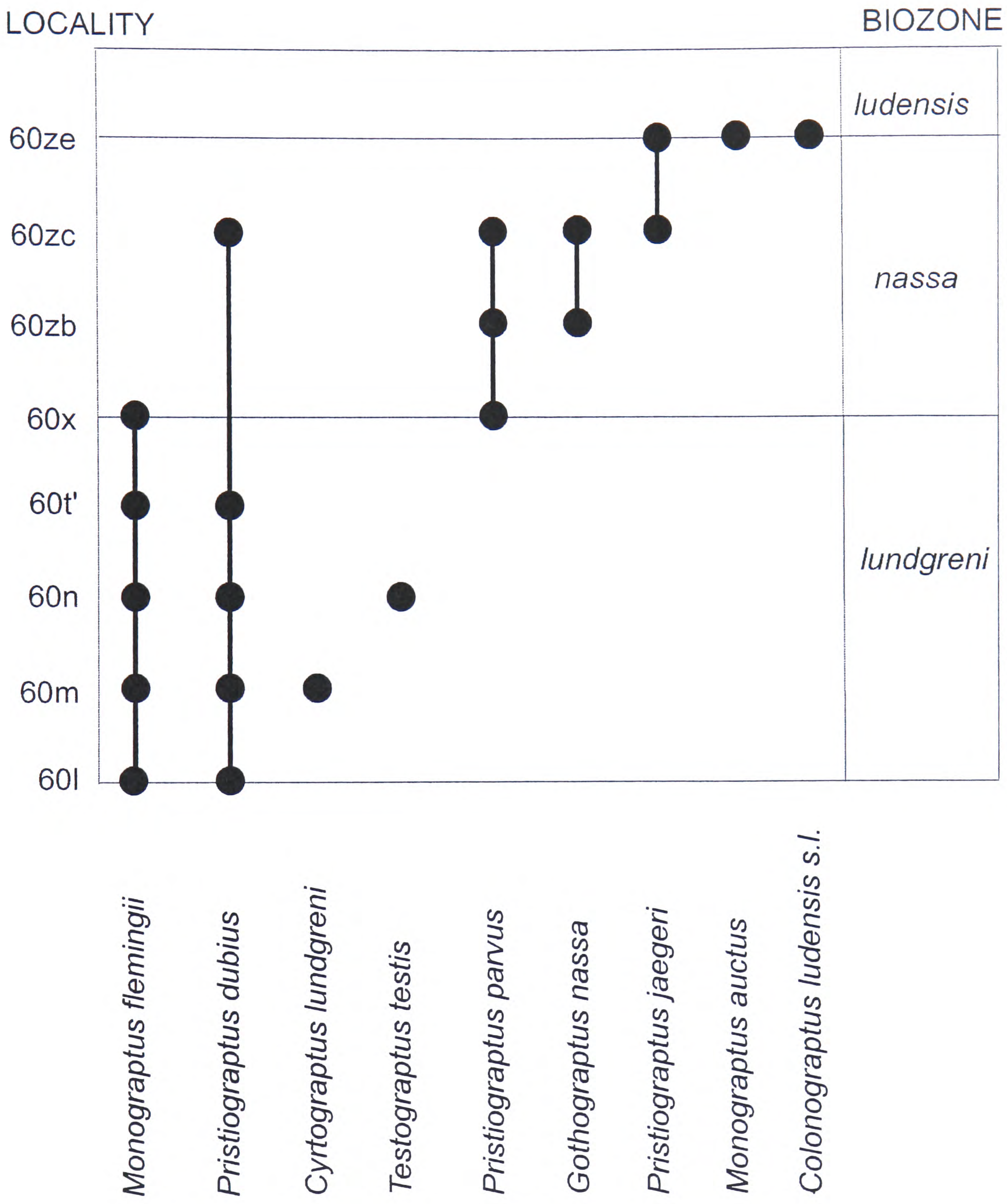


Figure 3.8: *Range chart of graptoloids in Douglas Palmer's collection. Exact vertical thicknesses are not shown.*

Between the *lundgreni* Zone and the *nassa* Zone there is a non-graptolitic interval containing a shelly fauna with abundant burrows. This is interpreted as having been deposited during a sea-level fall, because of the change from a graptoloid-nautiloid fauna to a shelly one. The presence of large burrow networks proves that the sea floor was oxygenated at this time. The presence of shelly benthos cannot be solely due to oxygenation, because Locality 8 is oxygenated (as proved by the presence of the same burrow networks), but the fauna is of graptoloids and nautiloids rather than shells.

The non-graptolitic interval lasted approximately 140 000 years, assuming a constant sedimentation rate. (The vertical thickness of the *lundgreni* Zone is 135 metres (measured from the map of Palmer 1972), the thickness of the shelly interval is 16 metres (Palmer 1972) and the *lundgreni* Zone has a duration of 1.2 million years (Kaljo *et al.* 1996).) This figure should not be taken as being precise, but does give an order of magnitude estimate of the duration of the non-graptolitic interval.

Some authors have said that the cause of the *lundgreni* extinction was an expansion in oceanic anoxia (Quinby-Hunt & Berry 1991), and some have said that a retreat in anoxia was responsible (Koren' 1987; Štorch 1995). These results do not support the former hypothesis, but are consistent with the latter. The environmental changes seen in Trewern Brook also occurred across the rest of the Welsh Basin - other sections from the Welsh Basin show a similar pattern to Trewern Brook, e.g. the Nantglyn Mudstones in the Rhayader area and Denbighshire (Warren *et al.* 1984 p.26; Davies *et al.* 1997 p.166-167). In Denbighshire, the Lower Mottled Mudstone is seen at the level of the *nassa* Zone, and the Upper Mottled Mudstone at the level of the *ludensis* Zone *s.l.* (Warren *et al.* 1984). In the Rhayader area, a single Mottled Mudstone Member, correlated with the Lower Mottled Mudstone of Denbighshire is seen (Davies *et al.* 1997). (This mottled mudstone is the highest bed seen in the district (Davies *et al.* 1997).) In both areas, the Nantglyn Mudstones are anoxic and the mottled mudstones are burrowed, indicating oxic conditions (Warren *et al.* 1984; Davies *et al.* 1997). A similar pattern is seen in the

Lake District with the Lower and Middle Coldwell Beds, which are calcareous bands in graptolitic mudstone of late *lundgreni* and *ludensis* Zone *s.l.* age (Rickards 1970). Thus the type of environmental changes seen in Trewern Brook, with anoxic conditions becoming oxic at the end of the *lundgreni* Zone, are seen across the whole of southern Britain.

Are these results of what occurred globally, or do they merely reflect local conditions? It appears that similar events happened in some areas, but not in others. A marker bed with no graptoloids at the end of the *lundgreni* Zone is seen in some places, for example Germany (Jaeger 1991) and Central Asia (Koren' 1991). However, this is not universal, for example Poland and Arctic Canada show no sedimentological changes at that horizon (Kozłowska-Dawidziuk *et al.* 2001). Unfortunately, details on the oxygenation status of graptolitic sections of this age from other countries are not available in the literature, so it is not possible to compare the pattern seen here with other regions. Further details are given in Section 2.8.

There are several possible explanations for the lack of graptoloids in the interval between the *lundgreni* and *nassa* zones. Firstly, the graptoloids went extinct – this may explain most of the disappearances, but not that of *Pristiograptus dubius*, because this species reappears in the *ludensis* Zone. Secondly, the graptoloids were there but were destroyed by the burrowing. However, identical burrows occur further up the sequence together with graptoloids (e.g. localities 8 and 31). Thirdly, the graptoloids migrated offshore into deeper water as the sea became shallower. This explanation is the most likely, because graptoloids are known to migrate during sea level changes (Goldman *et al.* 1999). A regression is seen in many areas at the end of the *lundgreni* Zone (Melchin *et al.* 1998).

In conclusion, short-lived (on a geological timescale) environmental changes occur at the time of the *lundgreni* event in the Welsh Borderland: a sea level fall and a change in the state of the sea floor from anoxic to oxic. This contradicts the hypothesis that the event was caused by the spread of anoxia in the oceans, and substantiates the hypothesis that the event was caused by the retreat of anoxia. This pattern applies across the Welsh Basin, but it is not known whether these changes are seen in other regions. Studies in other areas are required in order to test this.

4. Fieldwork in New South Wales, Australia

The graptoloid faunas of Australia are important in deducing what happened during the *lundgreni* extinction, because Australia appears to have acted as a refugium for graptoloids after the *lundgreni* event (Rickards & Wright 2002). Several genera (*Cyrtograptus*, *Testograptus* and *Monograptus s.s.*) are known from New South Wales after the end of the *lundgreni* Zone (Rickards *et al.* 1995a), whereas in the rest of the world they became extinct at the end of that zone. The graptoloids of Australia have not been worked on as much as those of Europe, so any contribution to their study is useful.

The aims of this part of the research were to study the sequence of events during the *lundgreni* extinction, especially environmental changes; to compare and contrast these with the events seen in the Welsh Borderland (Chapter 3); to describe the graptoloid fauna and to compare this fauna with others seen around the world. The first aim could not be fulfilled, due to poor exposure at the end of the *lundgreni* Zone in the studied sections.

In this chapter, two sections from the *lundgreni* Zone to the *ludensis* Zone *s.l.* are described. The *nassa* Zone was not seen. Both sections are in the Wellington-Canobolas District, near the town of Orange, New South Wales. One section is along Wallace Creek, thirty kilometres southwest of Orange, and the other is at One Tree Hill, twenty-five kilometres west of the town (Figure 4.1). Graptoloids have been known from the Orange area since the 1950s (Stevens & Packham 1953; Packham & Stevens 1955), and have been worked on in recent years by Rickards and co-workers (Rickards *et al.* 1995a; Rickards & Wright 1997). Taxonomic descriptions of some of the species present are given.

The Orange area is in the central eastern part of the Lachlan Fold Belt (Pogson & Watkins 1998). The Lachlan Fold Belt consists of alternating highs and troughs trending north-south (Figure 4.2). The Orange area is in the Hill End Trough. The

Hill End Trough was formed by tectonic movements associated with volcanism in the Early Silurian (Pogson & Watkins 1998). All the middle Late Silurian shelf sequences around the Hill End Trough are included in the Mumbil Group (Pogson & Watkins 1998). An outline of the stratigraphy of the relevant parts of the Mumbil Group is given in Figure 4.3. The Wallace Creek section is in the Ulah Formation and the One Tree Hill section is in the Mirrabooka Formation (Pogson & Watkins 1998). Limestones at the base of the Mumbil Group indicate deposition in shallow water, with the succeeding Ulah and Mirrabooka formations indicating deepening conditions (Pogson & Watkins 1998).

In previous studies, the rocks of both the One Tree Hill and the Wallace Creek areas have been placed in the Panuara Formation (e.g. Packham & Stevens 1955; Jenkins 1978; Rickards *et al.* 1995a). This formation was originally defined to include all the Silurian rocks below the Wallace Shale (Přidolí) (Packham & Stevens 1955). Jenkins (1978) and Rickards *et al.* (1995a) revised the definition of the formation but continued to use the name. The name is no longer in use, the current stratigraphy being that of Pogson & Watkins (1998), given above.

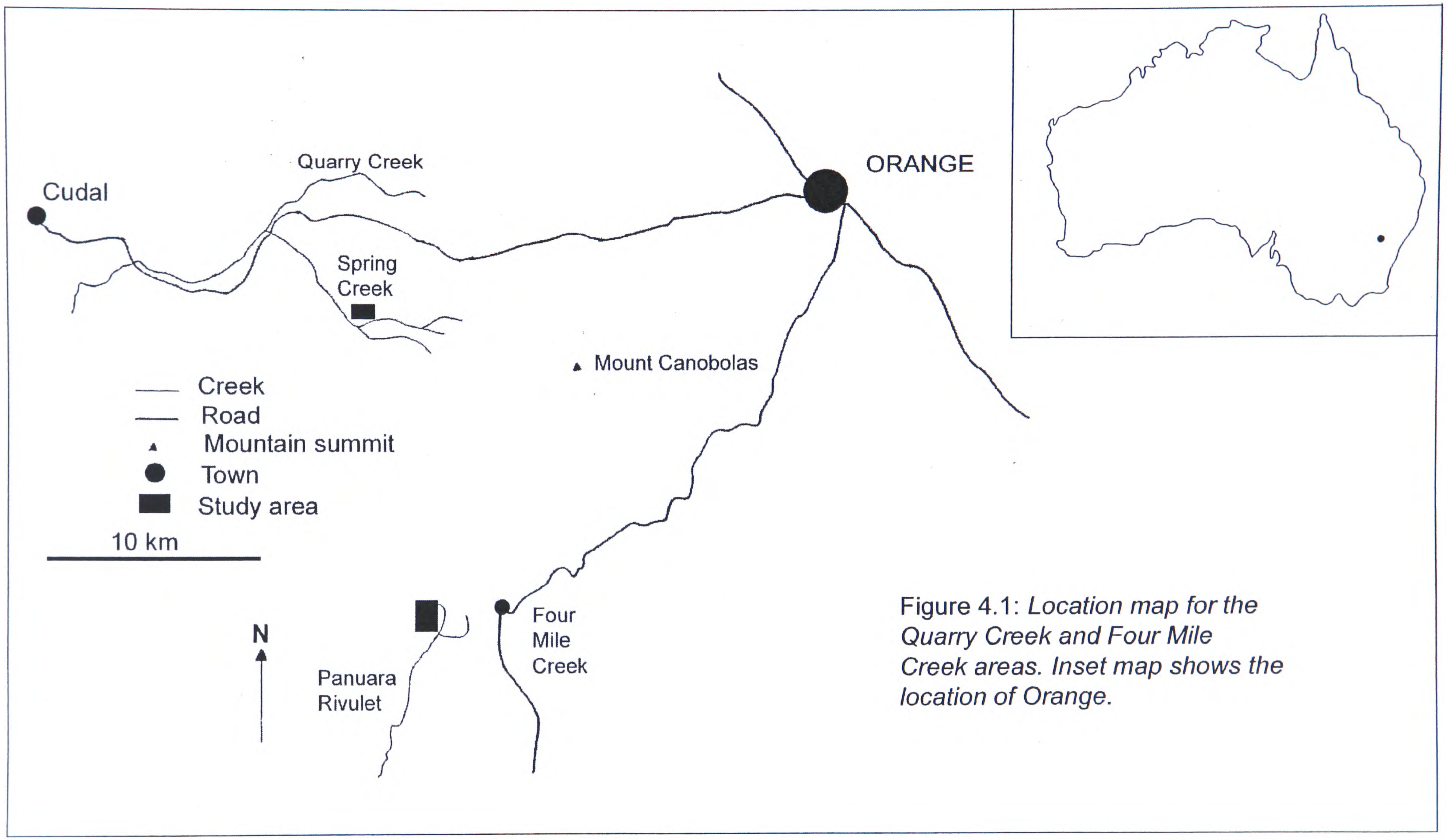


Figure 4.1: *Location map for the Quarry Creek and Four Mile Creek areas. Inset map shows the location of Orange.*

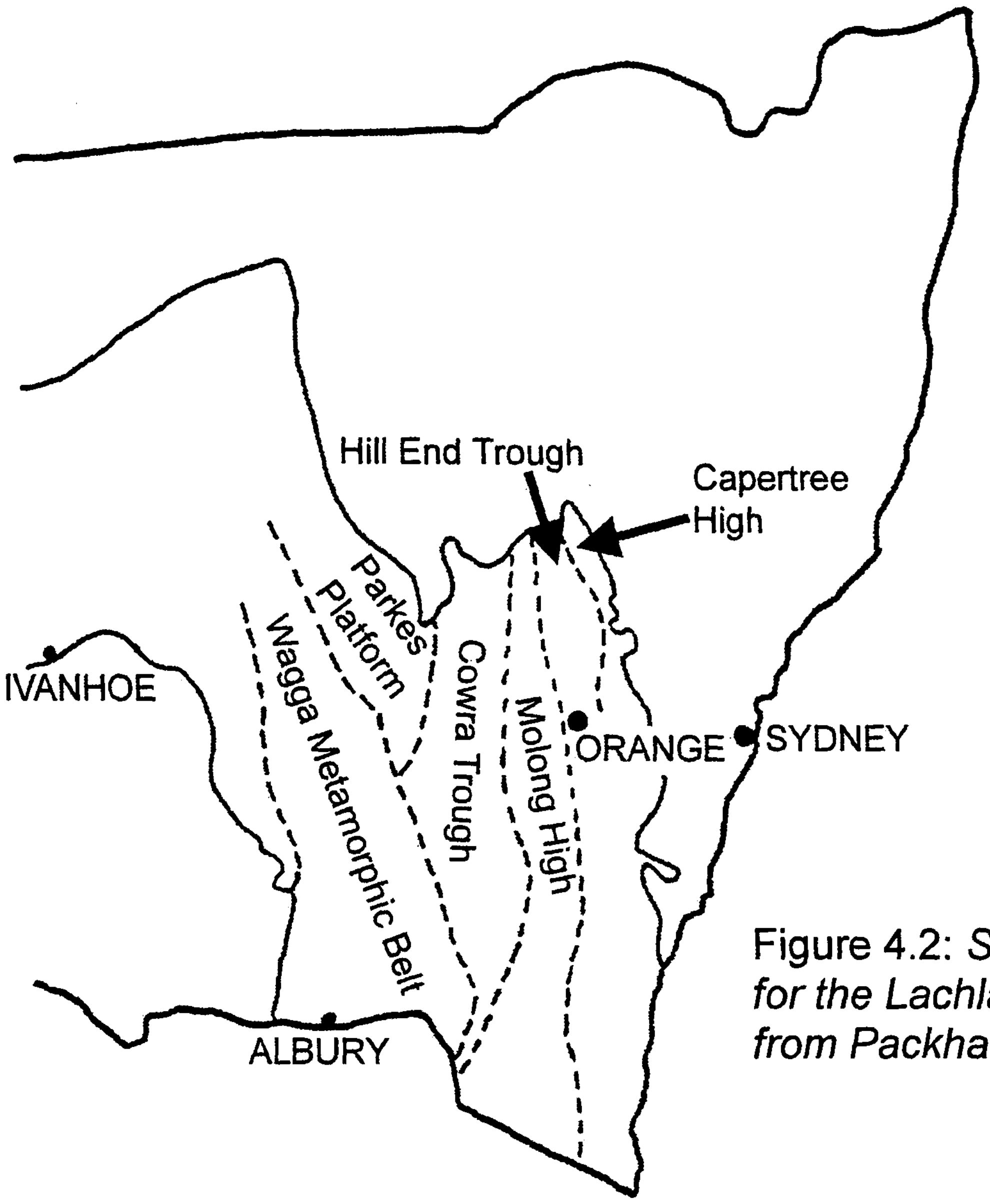


Figure 4.2: *Silurian palaeogeography for the Lachlan Fold Belt. Redrawn from Packham (1969).*

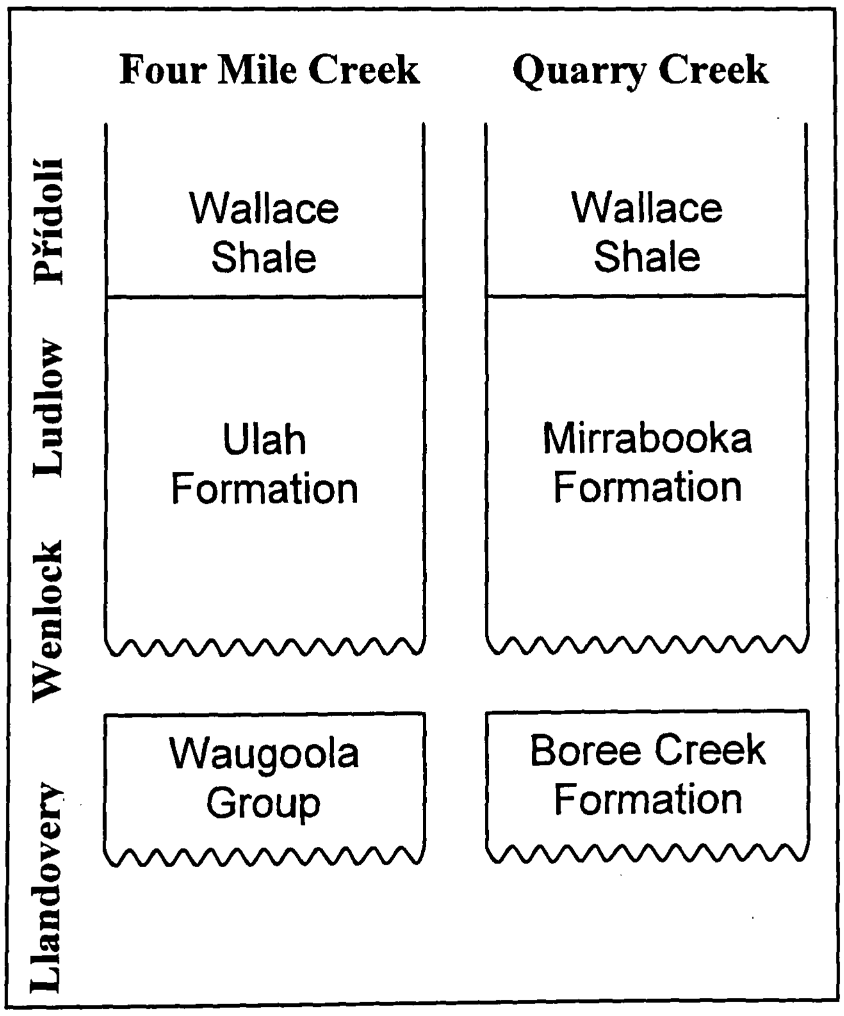


Figure 4.3: *Mumbil Group stratigraphy for the Four Mile Creek and Quarry Creek areas. Wallace Creek is in the Four Mile Creek area; One Tree Hill is in the Quarry Creek area.*

4.1 Wallace Creek

Wallace Creek is in the Four Mile Creek area, mapped by Packham & Stevens (1955) and Jenkins (1978). The graptoloid zones in this area range from the Llandovery *vesiculosus* Zone to the *ludensis* Zone *s.l.* (Jenkins 1978).

The localities collected from in this study are marked on Figure 4.4. The rocks are siltstone, brownish on unweathered surfaces, weathering grey, strike 000° and dip 80°W. Localities LM1 to LM3 are in the *lundgreni* Zone, and LM4 is in the *praedeubeli-deubeli* or *ludensis* zones, i.e. the *ludensis* Zone *s.l.* Exposure is poor above Locality LM2, and the transition between the *lundgreni* and *ludensis s.l.* zones was not exposed. Figure 4.5 gives a log of the Wallace Creek section. Locality LM1 contains abundant *Testograptus testis* and articulate brachiopods, and one nautiloid was collected. No other graptoloid species were found at this locality. Locality LM2 contains only fragments of graptolites. Locality LM3 contains a graptoloid fauna of *Pristiograptus* cf. *parvus*, *Cyrtograptus* sp., *Monograptus* sp. nov. (being described by Barrie Rickards), an indeterminate retiolitid, and also articulate brachiopods and dendroid fragments. This locality is heavily bioturbated. Locality LM4 contains *Colonograptus* ex gr. *ludensis* and articulate brachiopods.

Localities LM1 and LM3 are assigned to the *lundgreni* Zone because of the presence of *T. testis, Cyrtograptus* and *Monograptus*, and LM4 to the *ludensis* Zone *s.l.* on the basis of *C.* ex gr. *ludensis*. The base of the *ludensis* Zone *s.l.* has been drawn at locality LM4, but the actual base of the zone may be somewhat lower.

Testograptus testis specimens from Locality LM1 were used to construct a survivorship curve. Details of this are given in Section 6.2.5.

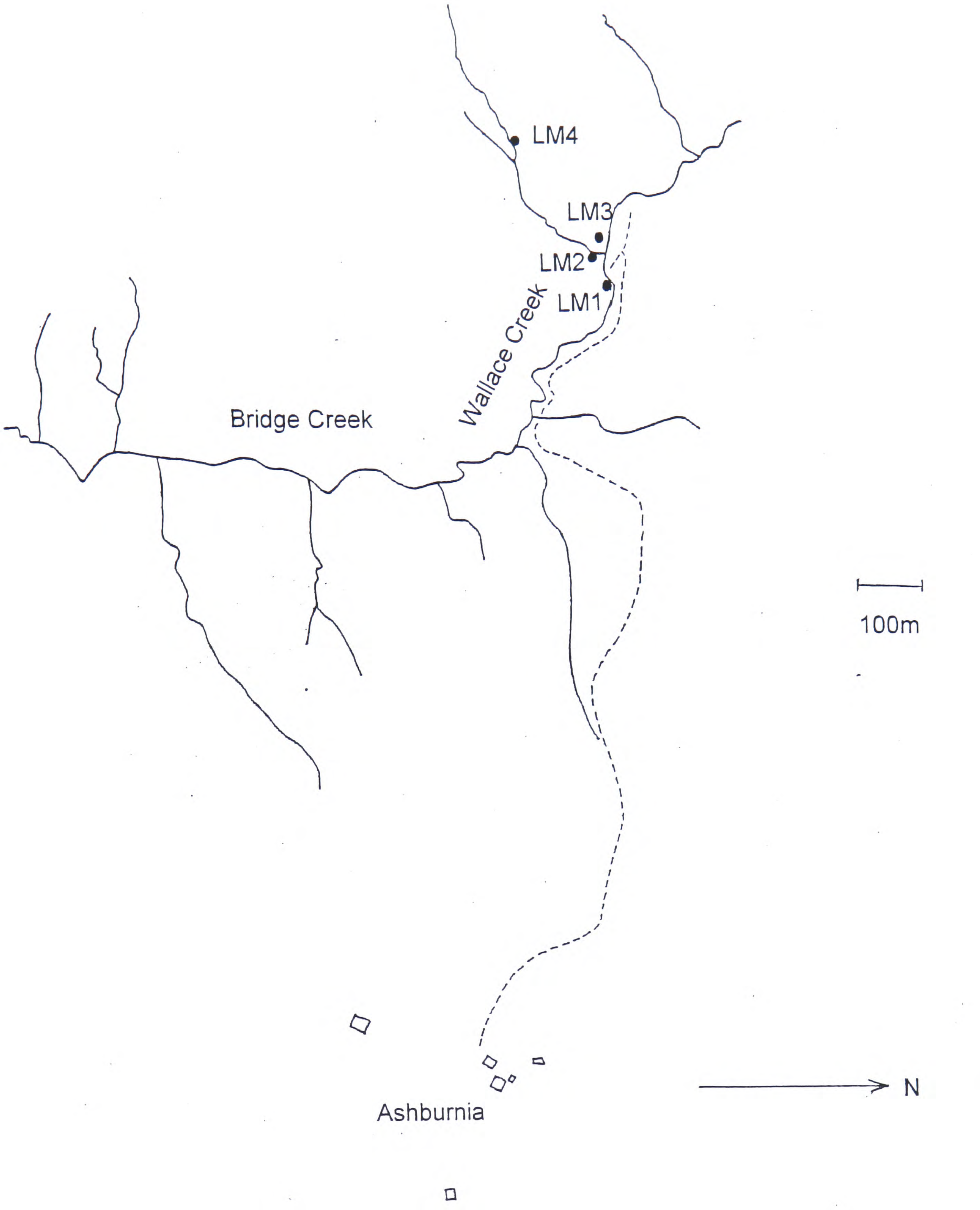


Figure 4.4: *Location map, Wallace Creek.*

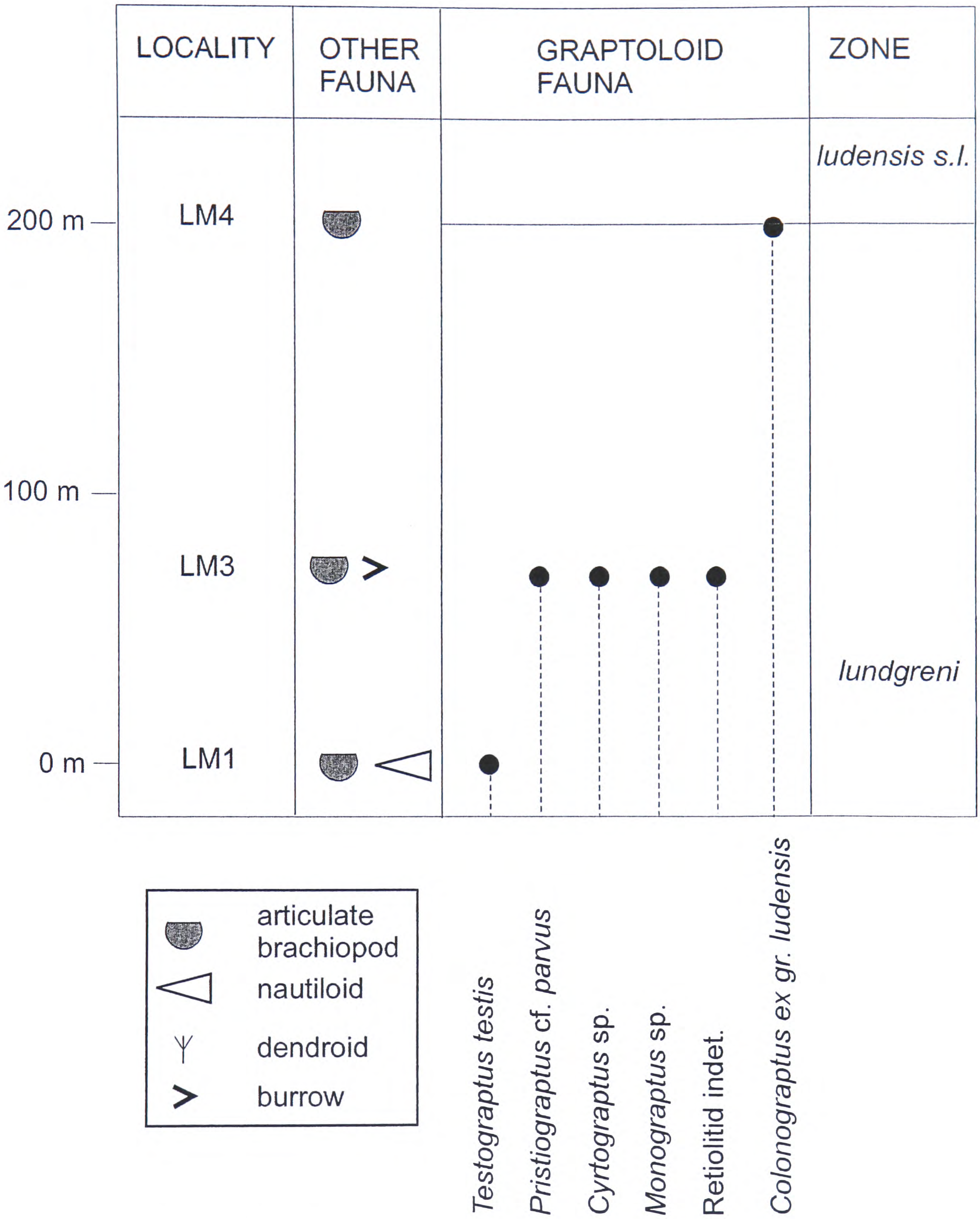


Figure 4.5: *Wallace Creek faunas. Locality 2 has been omitted as only fragments of graptolites were found there. Rock thicknesses are approximate.*

4.1.1 Faecal pellet

At Locality LM1 an oval object approximately 4.5mm long consisting of a mass of broken pieces of *Testograptus testis* was found (Figure 4.6A, B). The object is identified as a faecal pellet on the basis of its oval shape and the fact that it contains broken rhabdosomes. Figure 4.6C, D shows complete specimens of *T. testis* for comparison.

T. testis is a robust and spinose species, and it is therefore surprising that it was preyed upon – spines are generally thought to discourage predators. No graptoloids other than *T. testis* were present at this locality, so it is possible that the predator was simply taking the only thing available. The fact that such an apparently unpalatable species was preyed upon suggests that predation on graptoloids may have been more widespread than has been thought. It is possible that graptoloid predators were abundant wherever graptoloids were, but the evidence for their activity (faecal pellets) has not been preserved.

The identity of the predator is a mystery. Previous reports of predation on graptoloids (Loydell *et al.* 1998) involved very slender species, and the rhabdosomes being folded rather than broken. In this case the rhabdosomes were broken and the species is robust. Loydell *et al.* (1998) thought that predation in the examples they gave could not have been caused by conodonts or nautiloids, because the graptoloids were bent rather than broken. In this case the rhabdosomes are broken, so nautiloids or conodonts are possible predators. A nautiloid was found at this locality, but no conodonts were observed. A soft-bodied predator is also a possibility.

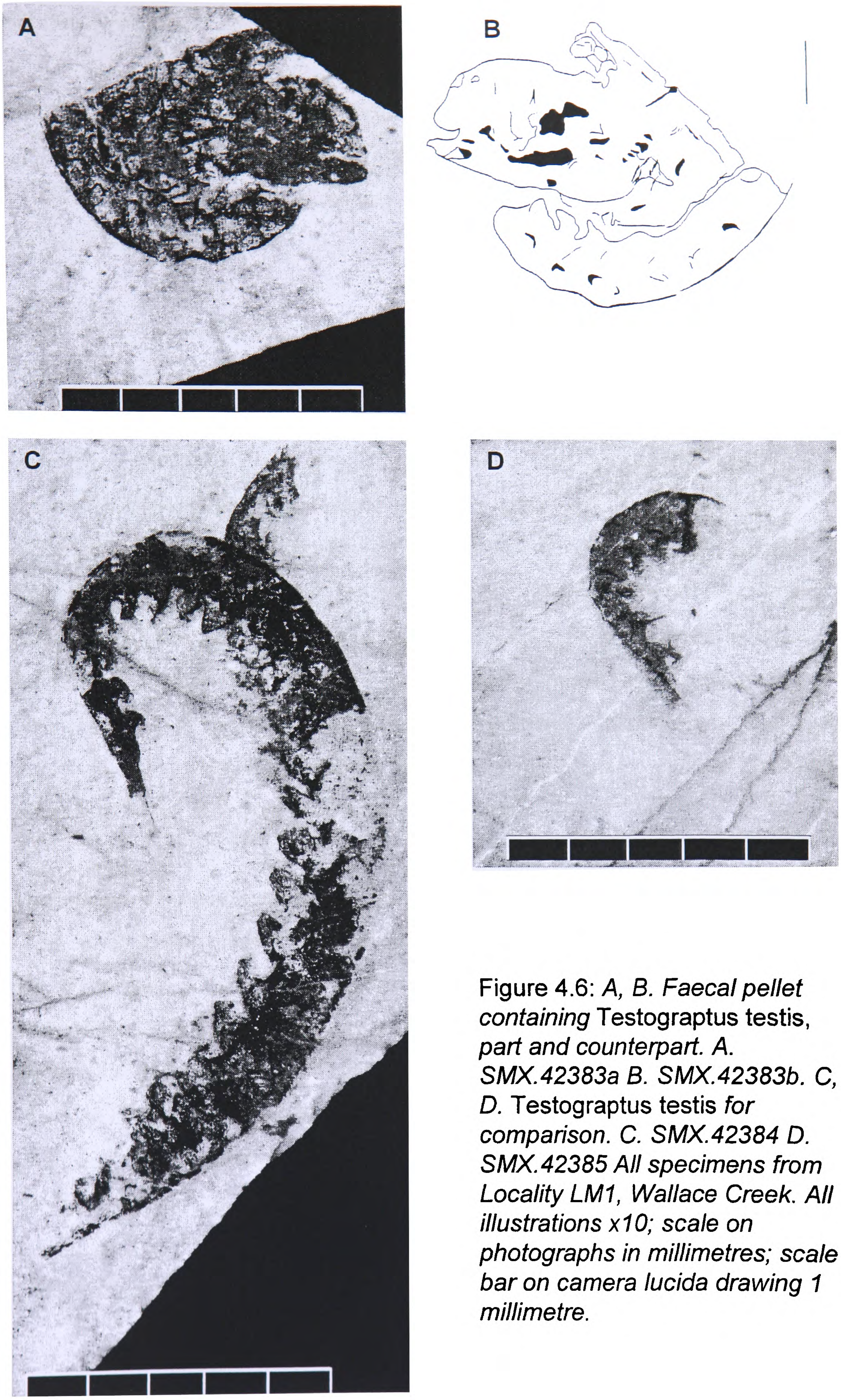


Figure 4.6: *A, B. Faecal pellet containing* Testograptus testis, *part and counterpart. A. SMX.42383a B. SMX.42383b. C, D.* Testograptus testis *for comparison. C. SMX.42384 D. SMX.42385 All specimens from Locality LM1, Wallace Creek. All illustrations x10; scale on photographs in millimetres; scale bar on camera lucida drawing 1 millimetre.*

4.2 One Tree Hill

One Tree Hill is a small hill beside Spring Creek, a tributary of Quarry Creek. The area was first mapped by Packham & Stevens (1955). Graptoloids from the Spring Creek area were mentioned by Jaeger (1991) and faunas were described in detail by Rickards *et al.* (1995a).

Figure 4.7 gives a location map for the section studied. A picture of the section is given in Figure 4.8, with a tracing showing some of the most striking features of the hillside and some localities. Figure 4.9 shows the faunas up the section. The lithology is mostly uniform light brown siltstone, with the exceptions of LM5A where the rock is a reddish siltstone and the outcrop below the rosebush, which is glauconitic sandstone. The strike is 024° and the dip 20°W. Exposure was reasonable in the lower part, although there was no exposure in the upper parts of the hill. As well as graptoloids, dendroids, articulate and inarticulate brachiopods, trilobites, bivalves and reticulosan hexactinellid sponges (J. Botting *pers. comm.*) occur (Figure 4.9). Parts of the section are bioturbated. This and the presence of benthos indicate that the environment was oxic. The section includes the *lundgreni* and *praedeubeli-deubeli* zones, but the *parvus-nassa* Zone was not recognised.

The *lundgreni* Zone is recognised at Locality LM5L by the presence of *Testograptus testis*. Although the preservation is poor, the distinctive rhabdosome shape of *T. testis* can be recognised. The apparent lack of other graptoloids may be due to poor preservation, or this locality may contain only *T. testis*, as at Locality LM1 of the Wallace Creek section. Locality LM5L is probably the same horizon described by Sherwin (1971) in the Cheesemans Creek district, 16 km west of Orange. He mentions "a bed of reddish cherty siltstone about 5 feet (1.5m) thick" containing sponge spicules and possible *Testograptus testis*; the same lithology and fauna as at LM5L. The One Tree Hill section is 25km west of Orange, so it appears that this bed occurs over a wide area, and thus may be useful for correlation.

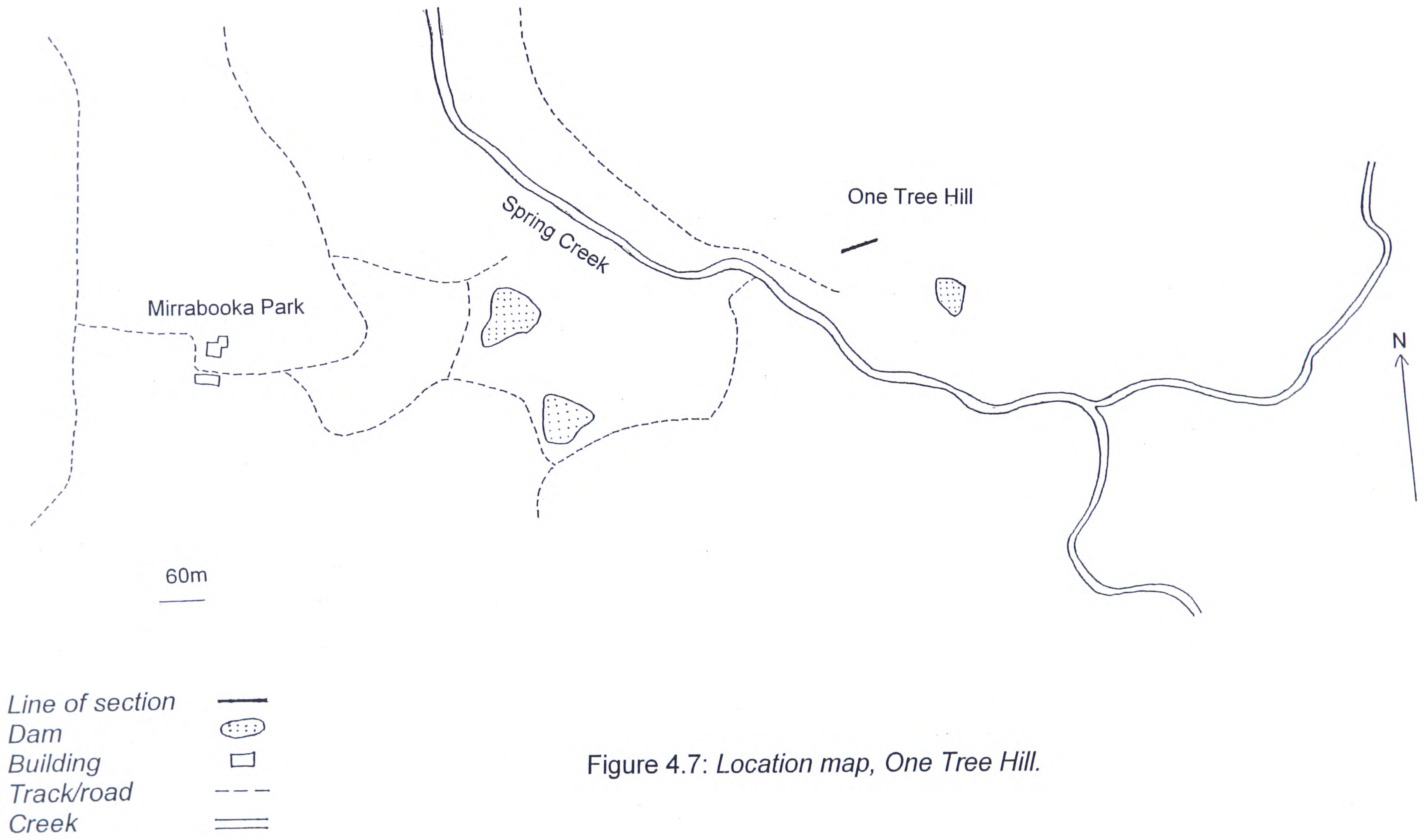


Figure 4.7: *Location map, One Tree Hill.*

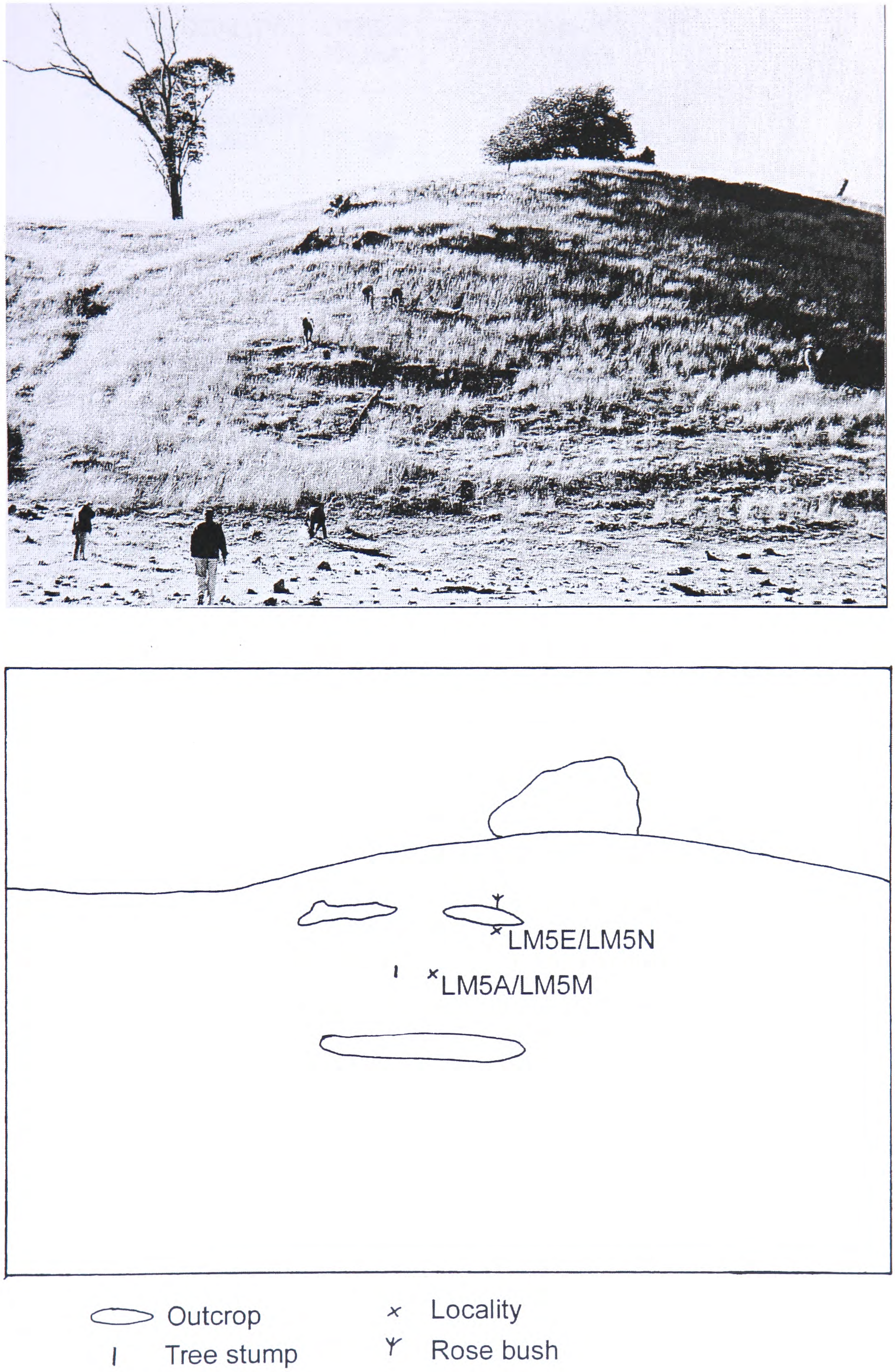


Figure 4.8: *Photograph of the One Tree Hill section and an explanatory tracing, from this photograph and field sketches.*

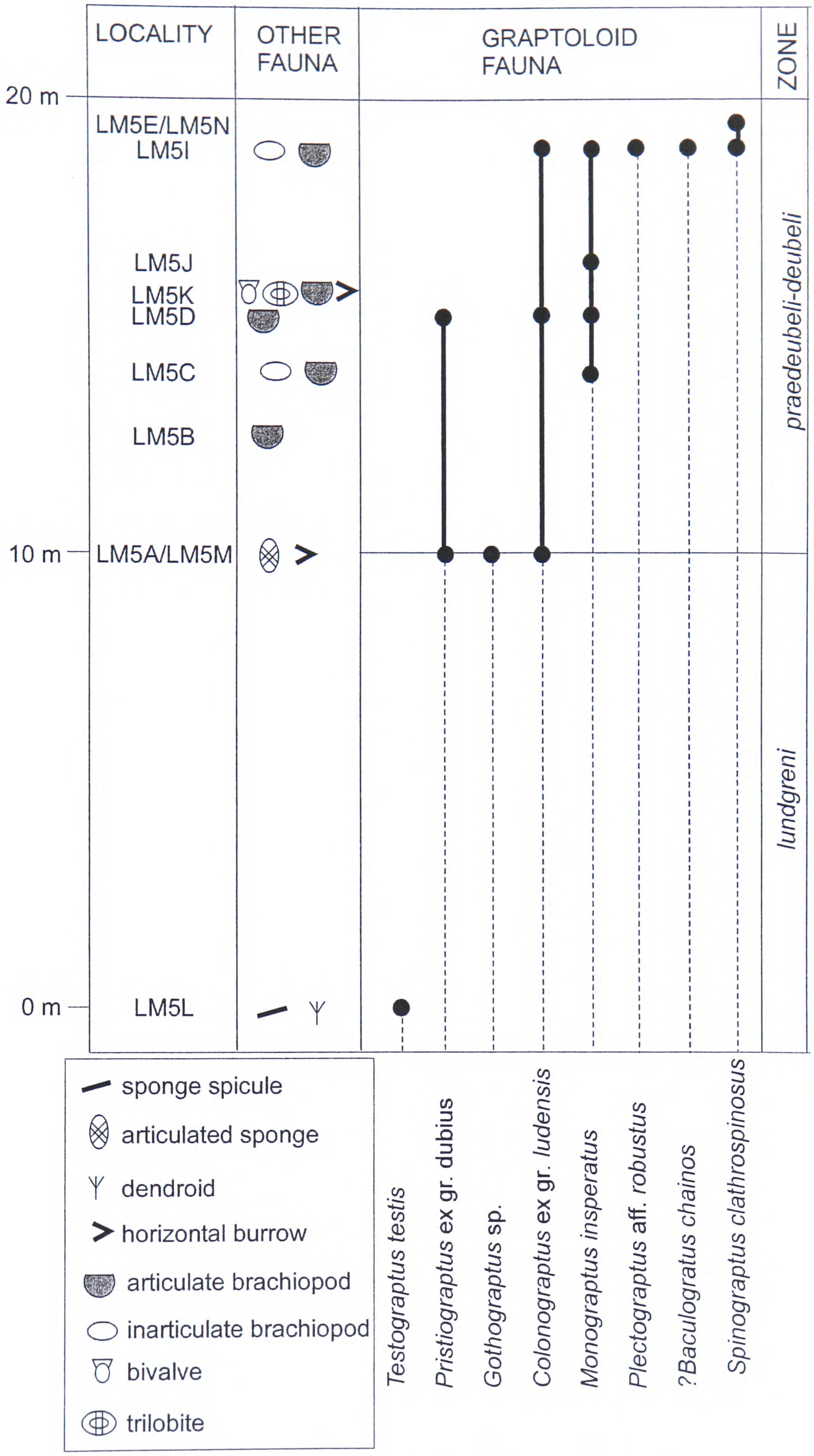


Figure 4.9: *One Tree Hill faunas. No fossils were found at Localities LM5F, LM5G and LM5H.*

The *praedeubeli-deubeli* Zone is recognised on the basis of the presence of *Colonograptus* ex gr. *ludensis* and *Monograptus insperatus*, which is known from the *sherrardae* (*praedeubeli*) Zone of central Asia (Koren' 1992). Species diversity appears to increase through the zone; this may be a real pattern, but could instead be an artefact of small sample sizes. The other graptoloids found are also known from this level in other areas. It is worth noting that Locality LM5A/LM5M would have been placed in the *parvus-nassa* Zone were it not for the occurrence of a single specimen of *Colonograptus* ex gr. *ludensis* there. The other graptoloids present at that locality are *Pristiograptus* ex gr. *dubius* and *Gothograptus* sp. A pristiograptid-gothograptid assemblage is characteristic of the *parvus-nassa* Zone.

4.3 *Ludensis* Zone *s.l.* hooked monograptids

Rickards *et al.* (1995a) figured four specimens named as *Monograptus* sp. ex gr. *M. flemingii* from the *ludensis* Zone *s.l.* of Spring Creek. This identification was queried by Lenz & Kozłowska-Dawidziuk (2001b, 2002b), who looked at some of the specimens and re-interpreted them as "some type of badly deformed pristiograptid." As this material is one of the few records of *Monograptus sensu stricto* in the *ludensis* Zone (see Section 2.4 for others), and so represents survivors of the *lundgreni* event, the correct identification of these specimens is important. In July 2002 I examined two of the specimens of *Monograptus* sp. ex gr. *M. flemingii* in the collection of Rickards *et al.* (1995a) in the Australian Museum, Sydney. The specimens seen were AMF81740 and AMF89589, both with part and counterpart. I could not find the other two specimens illustrated by Rickards *et al.* in the Australian Museum collection, and the specimens are not in the part of the collection that remained in the Sedgwick Museum, Cambridge (R.B. Rickards pers. comm. August 2002). The two specimens I saw are poorly preserved and lack proximal ends, and it is difficult to see details of the thecae. The specimens are illustrated as photographs in Rickards *et al.* (1995a, Figure 30). The thecae did not appear to be hooked, but did seem to be of pristiograptid type. Some specimens of the *Colonograptus ludensis* group have apertural lips (see for example Figure 4.10C), which might appear to be small hooks in poorly preserved material. AMF81740 appeared to possess these structures. In my opinion, the specimens I have seen are too poorly preserved to be identified with certainty, and therefore better specimens are required in order to confirm this possible record of *ludensis* Zone hooked monograptids.

4.4 Taxonomic descriptions

All the material described herein is deposited in the Sedgwick Museum, Cambridge, UK. In the retiolitid descriptions, the term clathrium is used to mean thick lists and reticulum to mean thin lists, after Lenz & Kozłowska-Dawidziuk (2001a). Use of open nomenclature (?, cf. and aff.) follows Bengtson (1988).

Order GRAPTOLOIDEA Lapworth in Hopkinson & Lapworth 1875
Suborder VIRGELLINA Fortey & Cooper 1986
Family RETIOLITIDAE Lapworth 1873

Retiolitid indet.
Figure 4.11E
Material: One poorly preserved specimen from Wallace Creek, SM X.42367.
Description: Rhabdosome parallel-sided, length at least 5.7mm, width excluding processes 1.3mm. Thecal count 12 in 10mm. Virgula free and central. Both clathrium and reticulum present. Thecal processes are present, but their structure could not be determined.
Remarks: The presence of a free central virgula and thecal processes might indicate membership of the genus *Cometograptus* Kozłowska-Dawidziuk 2001, but this specimen is too poorly preserved to be assigned with confidence to a genus.
Horizon: lundgreni Zone.

Subfamily PLECTOGRAPTINAE Bouček & Münch 1952

Baculograptus Lenz & Kozłowska-Dawidziuk 2002a

Type species: *Gothograptus chainos* Lenz 1993b

?*Baculograptus chainos* (Lenz 1993b)

Figure 4.10A

? *Gothograptus chainos* Lenz 1993b Plate 7 Figs. 1-12

? *Gothograptus chainos* Lenz 1994c Figs. 5.1-5.8

? *Gothograptus chainos* Rickards & Wright 1997 Fig. 5A-B

? *Baculograptus chainos* Lenz & Kozłowska-Dawidziuk 2002a Figs. 10.1-10.11

Material: One specimen, part and counterpart, from One Tree Hill, SM X.42360a-b.

Description: Rhabdosome 1.1mm wide medially, tapering slightly proximally and distally. Length 4.8mm. Thecae 13 in 10mm. Virgula central and free through most of the rhabdosome. Dense clathrium, no reticulum. Proximal and distal ends not preserved in this specimen.

Remarks: This material agrees with the type material in length and width, but has more thecae per 10mm (13 versus 10 for the type material). As just a single incomplete specimen is available, it is only questionably assigned to this species. The discovery of further material from this locality would permit a more certain identification.

Horizon: *praedeubeli-deubeli* Zone. The species has been found in the *sherrardae* (*praedeubeli*) Zone of New South Wales (Rickards & Wright 1997) and the *praedeubeli-deubeli* and *ludensis* zones of Arctic Canada (Lenz & Kozłowska-Dawidziuk 2002a).

Gothograptus Frech 1897

Type species: *Retiolites nassa* Holm 1890

***Gothograptus* sp.**

Figure 4.11G

Material: Two incomplete specimens from One Tree Hill, SM X.42361 and SM X. 42362a-b.

Remarks: No specific assignment is possible, because of the fragmentary nature of the material. The specimens are identified as *Gothograptus* on the basis of the meshwork structure.

Horizon: lower part of the *praedeubeli-deubeli* Zone.

Plectograptus Moberg & Törnquist 1909

Type species: *Retiolites macilentus* Törnquist 1887

Plectograptus* aff. *robustus (Obut & Zaslavskaya 1983)

Figure 4.10A

aff. *Agastograptus robustus* Obut & Zaslavskaya 1983 Plate XXIV Fig. 1-3

aff. *Agastograptus robustus* Obut & Zaslavskaya 1986 Figure 1a-c

Agastograptus robustus Rickards *et al.* 1995a Figure 18I, J

aff. *Plectograptus robustus* Kozłowska-Dawidziuk 2002 Figure 2C, D.

Material: Two flattened specimens on one slab from One Tree Hill, SM X.42363a-b and SM S.42364a-b.

Description: Rhabdosome oval in shape, over 8mm long. Maximum dorsoventral width excluding spines 2.5mm, including spines 3.1mm, falling to 1.25mm (excluding spines) distally. Thecal count 11 in 10mm. Free virgula projects beyond end of rhabdosome. Clathrium and reticulum present. Thecae bear paired processes: some appear to have traces of a reticulofusellar structure.

Remarks: The material described here agrees with the type in overall form and in the presence of thecal processes. It differs from that previously described in its width (2.5mm versus 2mm in the type) and the presence of reticulum; the type material (from the former Soviet Union) and other material from Poland do not possess reticulum (Obut & Zaslavskaya 1983; Kozłowska-Dawidziuk 2002). Material described by Rickards *et al.* (1995a) as *Agastograptus robustus* from the Quarry Creek area does possess reticulum, but differs slightly from the present material in its narrower maximum dorsoventral width (2mm) and thecal spacing (14 in 10mm proximally, 12 in 10mm distally). However, as the material of Rickards *et al.* (1995a) consisted of only two specimens, these differences may merely reflect inadequate sampling of a variable population.

Spinograptus praerobustus Lenz & Kozłowska-Dawidziuk 2002a is a similar species to *Plectograptus robustus*, but differs from the material described here in its absence of reticulum and smaller maximum width (1.3-1.5mm) (Lenz & Kozłowska-Dawidziuk 2002a).

Horizon: praedeubeli-deubeli Zone. This species is otherwise known from the *ludensis* Zone *s.l.* of Poland and the *nilssoni* Zone of Kaliningrad, Russia (Kozłowska-Dawidziuk 2002).

Spinograptus Bouček & Münch 1952

Type species: *Retiolites spinosus* Wood 1900

Spinograptus clathrospinosus (Eisenack 1951)

Figure 4.11F

Retiolites clathrospinosus Eisenack 1951 Plate XXIII, Fig. 1-2

Agastograptus clathrospinosus Obut & Zaslavskaya 1983 Plate XXV Fig. 1-3

Agastograptus clathrospinosus Obut & Zaslavskaya 1986 Fig. 2a-c

Agastograptus clathrospinosus Lenz 1993b Plate 3 Fig. 1-7, Plate 4 Fig. 1-9

Agastograptus clathrospinus Rickards *et al.* 1995a Fig. 18D

Spinograptus clathrospinosus Kozłowska-Dawidziuk *et al.* 2001 Figs. 5.9, 5.13, 5.15, 7.6

Spinograptus clathrospinosus Lenz & Kozłowska-Dawidziuk 2002a Figs. 13.6-13.8, 14.7, 14.10, 16.13-16.15

Material: Two incomplete specimens from One Tree Hill, SM X.42365 and SM X.42366a-b.

Description: Rhabdosome straight-sided, 0.9-1.1mm wide excluding apertural processes. Rhabdosome length at least 3.9mm. Thecal count 14½ in 10mm. Apertural processes 1.2mm long, with reticulofusellar structure.

Remarks: These specimens are identified as *Spinograptus* on the basis of the presence of apertural processes with reticulofusellar structure. They are assigned to *S. clathrospinosus* because of the rhabdosome dimensions and straight-sidedness.

Horizon: praedeubeli-deubeli Zone. This species is also known from the *nassa* Zone of Kaliningrad, the *praedeubeli-deubeli* Zone of Arctic Canada and the *nilssoni* Zone of Eastern Europe (Lenz & Kozłowska-Dawidziuk 2002a).

Family MONOGRAPTIDAE Lapworth 1873

Subfamily MONOGRAPTINAE Bouček 1933

Colonograptus Přibyl 1942

Type species: *Colonograptus colonus* Barrande 1850

Colonograptus ex gr. ludensis (Murchison 1839)

Figures 4.10C, 4.11A, B

ex gr. *Colonograptus*? *ludensis* Lenz 1995 Figs. 9D-I, 11N, O, W, X

ex gr. *Monograptus ludensis* Rickards *et al.* 1995a Figs. 26J, L-Q, 27F-H, 28A, B

ex gr. *Monograptus ludensis* Rickards & Wright 1997 Figs. 2D, E, H, 4A-E, 5J (?Figs. 2F, G)

ex gr. *Colonograptus ludensis* Lenz & Kozłowska-Dawidziuk 2002a Figs. 18.9, 18.10, 18.12, 18.13 (?18.11)

Material: 7 flattened specimens: SM X.42368-42372 and SM X.42386 from One Tree Hill and SM X.42373a-b and SM X.42374 from Wallace Creek.

Description: Rhabdosome robust, straight or slightly ventrally curved. Length up to at least 9mm. Width at th1 0.7-1mm, th2 0.8-1.1mm, th3 0.7-1.3mm, th4 0.8-1.3mm, th5 1-1.3mm, maximum 1.3-2mm. Thecal spacing 14-18 in 10mm proximally, 10-15 in 10mm distally. Sicula ventrally curved, 1.3-2.0mm long, apertural width 0.2-0.3mm. Apex reaches between aperture of th1 and middle of th3. Thecae simple tubes, th1 and th2 slightly rounded. On the more robust specimens thecae have thickened apertural lips. Thecal angle 27-47° proximally, 28-41° distally.

Remarks: The *Colonograptus ludensis* group (C. *ludensis, C. praedeubeli* and *C. gerhardi*) can be distinguished from other species by the rounding of the first few thecae, slight ventral curvature of the sicula and proximal end and the distal thecae being simple tubes. Within the group there is some disagreement over whether *C. praedeubeli, C. ludensis* and *C. gerhardi* can be distinguished as separate species or are different growth stages of one species. Rickards & Wright (1997) figured a series of growth stages of *C. ludensis* from the type slab, corresponding to *C. praedeubeli* (youngest) to *C. gerhardi* (oldest), showing increased dorso-ventral width and thecal length and changes in thecal morphology. However, other workers (e.g. Lenz 1995; Lenz & Kozłowska-Dawidziuk 2002a) have distinguished the different species on the basis of the length of the sicula and the thecal angle, *C. praedeubeli* having a longer sicula and lower thecal angle than *C. ludensis*. Sicula length and thecal angle (if measured dorsally rather than at the aperture) do not change during astogeny, hence these characters cannot be different at different growth stages. All workers agree that the morphs/species intergrade. As Jaeger (1991) pointed out, this is exactly what would be expected in an evolving lineage.

The question of whether or not the species currently distinguished represent growth stages of a single species or separate (but intergrading) species is an important one, particularly because the group has been extensively used in biostratigraphy. A large-scale statistical study would settle the matter of whether or not separate species are distinguishable. Some characters, such as dorso-ventral width, can change during astogeny, but some, such as thecal spacing and where the apex of the sicula reaches, cannot. The latter characters are the ones that should be used when deciding whether or not more than one species exists. In addition, material from several different places and times should be used, because material from a single place at a single time may not be representative of the entire lineage over several biozones.

This material agrees closely with that from Quarry Creek described as *C. ludensis* by Rickards *et al.* (1995) and the Canadian Arctic material described by Lenz (1995). Even if separate species do exist, distinguishing them requires large collections, hence all the specimens here are ascribed to *C.* ex gr. *ludensis.* The specimens from Wallace Creek have a slightly larger sicula and greater dorso-ventral width than those from One Tree Hill (see Table 4.1), and probably represent *C. ludensis* s.s.

Horizon: praedeubeli-deubeli Zone, One Tree Hill; *ludensis* Zone *s.l.*, Wallace Creek. The *Colonograptus ludensis* group is abundant and widespread during the late Homerian (see Appendix 3 for references).

Table 4.1: Colonograptus *ex gr.* ludensis *measurements. All measurements in millimetres, thecal spacings are number of theca in 10mm. "Width" means dorso-ventral width. X = could not be measured on that specimen.*

Specimen	Rhabdosome length	Width th1	Width th2	Width th3	Width th4	Width th5	Maximum width
LM5D.06	9	0.8	0.8	0.7	0.8	1.0	1.3
LM5I.20	2.2	0.9	0.9	1.0	X	X	X
LM5I.12	4.3	0.9	0.9	1.1	1.2	1.5	X
LM5M.09	7.7	0.7	0.8	0.9	1.0	1.0	1.3
LM4.05	9.1	1.0	1.1	1.1	1.2	1.3	1.7
LM4.03	6.8	1.0	1.1	1.3	1.3	1.5	2.0

Specimen	Sicula length	Sicula apertural width	Sicula reaches	Thecal spacing proximally	Thecal spacing distally	Thecal angle proximally	Thecal angle distally
LM5D.06	1.8	0.3	th2 aperture	15	10	27°	28°
LM5I.20	1.3	0.3	th1 aperture	17	X	47°	X
LM5I.12	X	X	X	14	X	47°	X
LM5M.09	X	0.2	X	16	13	33°	36°
LM4.05	1.9	0.3	th2 aperture	17	12	31°	31°
LM4.03	2.0	0.3	th3 middle	18	15	41°	40°

Monograptus Geinitz 1852

Type species: *Lomatoceras priodon* Bronn 1835

Monograptus insperatus Koren' 1992

Figure 4.10B, D

Monograptus insperatus Koren' 1992 p. 29, Fig. 5ж, 5з, 5и, 5к, Plate 3 Fig. 6-9

Monograptus insperatus Rickards & Sandford 1998 p.756 Fig. 8a

Material: Four flattened specimens from One Tree Hill: two complete (SM X.42375 and SM X.42376a-b) and two incomplete (SM X.42377a-b and SM X.42378a-b).

Description: Small, slender monograptid. Rhabdosome length 7.5mm. Dorso-ventral width at th1 0.7-0.8mm, widening to a maximum of 1.4 mm at th9. Rhabdosome slightly ventrally curved. Thecae bear lappets. Thecal spacing 14-15 in 10mm proximally, 12 in 10 mm distally. Sicula 1.5mm long, ventrally curved with prominent virgella. Apex reaches between base of th2 and base of th3. Sicula apertural width 0.25mm.

Remarks: The material described here differs slightly from previously described material. For the specimens described here, the sicula is smaller than previously described material (2.10-2.25mm in the type material). The dorso-ventral width is slightly less (1.85mm in the specimen described by Rickards & Sandford (1998), 1.5-1.6mm in the type material), but this is probably not significant as the Rickards & Sandford specimen was gerontic (Rickards & Sandford 1998), and the type material includes longer (and therefore wider specimens) than that seen here. Also, the specimens here have slightly ventrally curved rhabdosomes, rather than straight ones.

This is the first record of this species from New South Wales, the second from Australia and the third worldwide. The species has previously been described from central Asia (Koren' 1992) and Victoria (Rickards & Sandford 1998).

Horizon: praedeubeli-deubeli Zone. The species is previously known from the *sherrardae* (*praedeubeli*) Zone of Central Asia. The exact locality of the specimen from Victoria is unknown, and was attributed to "probably *ludensis* Biozone" (Rickards & Sandford 1998).

Pristiograptus Jaekel 1889

Type species: *Pristiograptus frequens* Jaekel 1889

Pristiograptus* cf. *parvus Ulst 1974

Figure 4.11C, D

non *Monograptus pseudodubius* Bouček 1932 Fig.2e, f

cf. *Pristiograptus parvus* Ulst 1974 Plate XI Fig. 5, Plate XII Fig. 3

cf. *Pristiograptus pseudodubius* Rickards 1965 Plate 29 Fig. 10, text-fig 2i

cf. *Pristiograptus parvus* Rickards *et al.* 1995a Figures 22K-M, 23D-H, 25C

cf. *Pristiograptus parvus* Radzevičius & Paškevičius 2000 Plate 6 Fig. F (?Plate 2 Fig. 2a, b, 3a, b)

cf. *Pristiograptus parvus* Kozłowska-Dawidziuk *et al.* 2001 Figs. 8.11-8.13, 9.6-9.8

Material: Four flattened specimens from Wallace Creek: SM X.42379-42382.

Description: Small, slender pristiograptid. Rhabdosome straight distally, straight or slightly ventrally curved proximally. Rhabdosome length up to 8.5mm, width at th1 0.4-0.7mm, widening gradually to a maximum of 0.7-0.8mm. Thecae simple tubes, spacing 12½-15 in 10mm. Thecal angle 19-27°. Sicula straight or ventrally curved, 0.8-1.5mm long, apertural width 0.3mm.

Remarks: This material differs slightly from the type; there are more thecae in 10mm and the thecal angle is smaller. The type material has 11-12 thecae in 10mm and a thecal angle of 30° (Ulst 1974). In addition, these specimens have a more variable width at th1 (0.4-0.7mm as against 0.5-0.6mm for the type material (Ulst 1974)), and their maximum width is less (0.7-0.8mm, the type is 0.7-1.0mm (Ulst 1974)). Material previously described from the Orange area (Rickards *et al.* 1995a) is similar to these specimens, but has a longer sicula (up to 2mm) and fewer thecae per 10mm (9-11/10mm).

P. parvus can be distinguished from other pristiograptids on the basis of its dorso-ventral width, which does not exceed 1mm except in the longest specimens.

Rickards *et al.* (1995a) stated that they considered *Pristiograptus pseudodubius* (Bouček 1932) to be a junior synonym of *P. parvus*, even though *P. pseudodubius* was described first. At least some identifications of *P. pseudodubius*

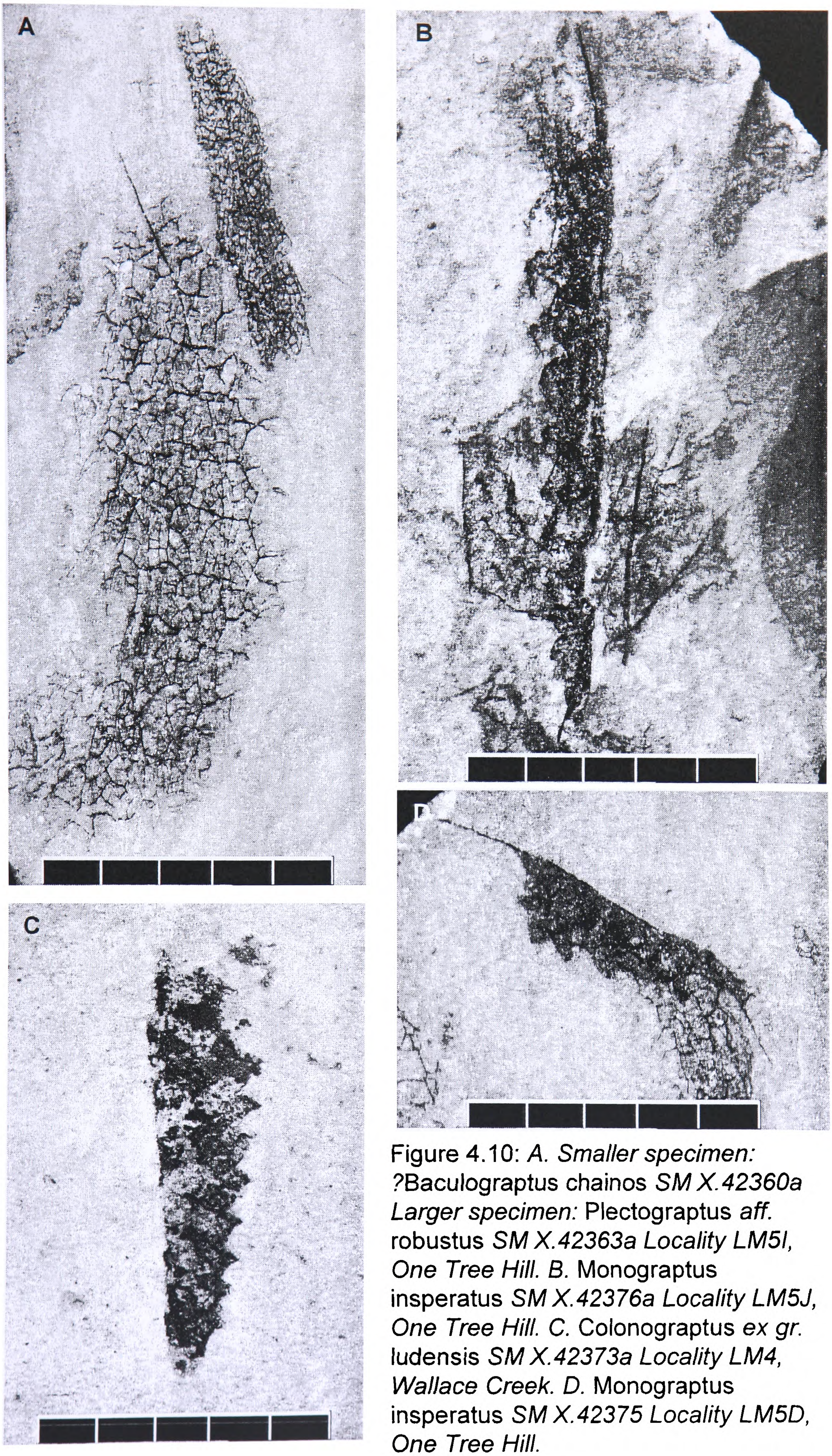


Figure 4.10: *A. Smaller specimen:* ?Baculograptus chainos *SM X.42360a Larger specimen:* Plectograptus *aff.* robustus *SM X.42363a Locality LM5I, One Tree Hill. B.* Monograptus insperatus *SM X.42376a Locality LM5J, One Tree Hill. C.* Colonograptus *ex gr.* ludensis *SM X.42373a Locality LM4, Wallace Creek. D.* Monograptus insperatus *SM X.42375 Locality LM5D, One Tree Hill.*

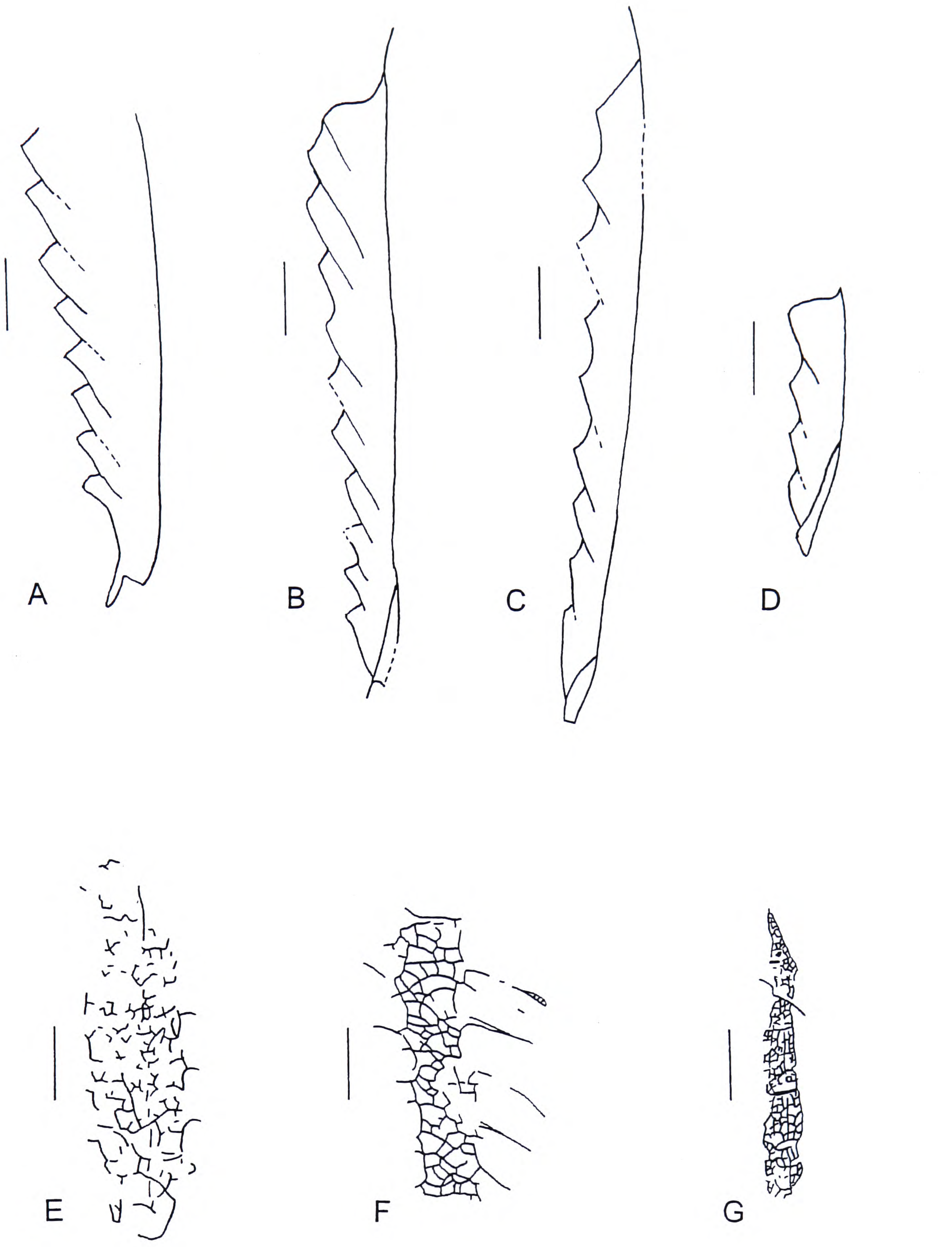


Figure 4.11: *A, B.* Colonograptus *ex gr.* ludensis *A. SM X.42374 Locality LM4, Wallace Creek B. SM X.42386 Locality LM5D, One Tree Hill. C, D.* Pristiograptus *cf.* parvus *C. SM X.42380 D. SM X.42379 both Locality LM3, Wallace Creek. E. Retiolitid indet. SM X.42367 Locality LM3, Wallace Creek. F.* Spinograptus clathrospinosus *SMX.42366a Locality LM5N, One Tree Hill G.* Gothograptus *sp. SMX.42361 Locality LM5M, One Tree Hill. All drawings x10, scale bar 1mm in each case.*

are misidentifications of *P. parvus* (e.g. Rickards 1965), but the fact that *P. pseudodubius* has been misidentified does not make it an invalid species. The type specimen of *P. pseudodubius* is distinct from *P. parvus*, being more robust and longer (1.2mm dorso-ventral width). Unfortunately Bouček only illustrated the type specimen and a distal fragment, so it is impossible to know the range of variation within the species. The original description of *P. pseudodubius* is "This species represents a remarkably small and narrow *M. dubius* (Suess), and should be regarded as a degenerate form to the type. Length 20-30mm, width 1mm, which it attains at the greatest distance from the sicula. Other features as in *M. dubius*" (Bouček 1932 p.152). This description fits *P. parvus* in the features given, but does not agree with the illustrated type specimen. I conclude that *P. parvus* and *P. pseudodubius* are not synonyms, but a revision of *P. pseudodubius* would be a worthwhile exercise. *Horizon: lundgreni* Zone. *P. parvus* is widely known from the *parvus-nassa* Zone in Europe (e.g. Kaljo *et al.* 1984; Gutierrez-Marco *et al.* 1996; Kozłowska-Dawidziuk 1999).

4.5 Conclusions

Three monograptid and four retiolitid species were found in the *praedeubeli-deubeli* Zone. The diversity of monograptids is lower than that seen in some other areas (ten species are found in Arctic Canada (Lenz 1995; Lenz & Kozłowska-Dawidziuk 2002a) and seven in central Asia (Koren' 1991)). In contrast, the retiolitid diversity is as high or higher than that of most places. The highest diversity known in the world at this time is thirteen species in Arctic Canada (Lenz 1995; Lenz & Kozłowska-Dawidziuk 2002a), but other than this greatest known is four species in the Czech Republic (Kozłowska-Dawidziuk *et al.* 2001) and Germany (Jaeger 1991). In this study the number of retiolitids found was strongly affected by collecting bias - only one retiolitid was seen in the field; all the other specimens were noticed under the microscope. Undoubtedly many specimens were unwittingly left on the outcrop. This means that the actual diversity of retiolitids at this locality is probably more than four species; many more would be found with further collecting. Bulk sampling would be an appropriate collecting method; not only would this technique avoid leaving retiolitids on the outcrop, but would result in unbiased collections, which could be used for population studies.

The numbers of individuals collected for each species are low, with the maximum being seven specimens of *Colonograptus* ex gr. *ludensis*. No attempt was made at a population study, because of the high degree of collecting bias and the small total number of specimens.

Most of the monograptids found are cosmopolitan, with the exception of *Monograptus insperatus*, which is currently only known from Central Asia and Victoria, Australia (Koren' 1992; Rickards & Sandford 1998). The retiolitids appear to have a more restricted distribution. *Baculograptus chainos* is known only from Arctic Canada and New South Wales (Lenz & Kozłowska-Dawidziuk 2002a; Rickards & Wright 1997), and *Plectograptus robustus* is known from Europe but not from Arctic Canada (Kozłowska-Dawidziuk 2002). (The specimens attributed to *Plectograptus robustus* by Lenz (1994c, 1994d), are now assigned to *Spinograptus praerobustus* (Lenz & Kozłowska-Dawidziuk 2002a).) *S. clathrospinosus* is found both in Arctic Canada and Europe (Lenz & Kozłowska-Dawidziuk 2002a). Thus it appears that Australian faunas have affinities with those of Europe, Central Asia and Arctic Canada.

In this study, no *lundgreni* Zone species, with the exceptions of *Pristiograptus* ex gr. *dubius* (found globally throughout the Homerian) and *Spinograptus clathrospinosus* (found in Arctic Canada during the *lundgreni* Zone and widespread in the *ludensis* Zone *s.l.* (see Appendix 3 for references)), were found in the *praedeubeli-deubeli* or *ludensis s.l.* zones. Previous studies in this area (Jenkins 1978; Rickards *et al.* 1995a) have found *lundgreni* Zone survivors not found elsewhere in the *ludensis* Zone *s.l.*, e.g. *Testograptus testis* and *Monograptus flemingii*. This failure to find any *lundgreni* Zone survivors suggests that they were extremely uncommon at this time.

The first appearance of *Pristiograptus parvus* is used as a marker for the base of the *parvus-nassa* Zone (Koren' *et al.* 1996). However, the presence of a *parvus*-like form in the *lundgreni* Zone of Wallace Creek, as well as *P. parvus* in the *lundgreni* Zone of Trewern Brook (Chapter 3), suggests that zonal definitions may need to be revised. *Gothograptus nassa* and *Pristiograptus dubius*, the other species common in the *parvus-nassa* Zone, are also found in the *lundgreni* Zone, although records of *G. nassa* have been disputed (Section 2.1). Thus there is no suitable species whose first appearance could be used as a marker for the base of the zone. The zone was originally defined as an interval biozone (Jaeger 1991), and may have to be defined on that basis again. In this case, the zone would be defined as the interval between the vanishing of the *lundgreni* Zone fauna and the incoming of the *ludensis* Zone *s.l.* fauna. Interval biozones are unsatisfactory from a biostratigraphical point of view, because they are recognised by the absence, rather than the presence, of species and so there is always the possibility that further collecting will turn up a single specimen of another species and completely alter the zonation. However, at times of high extinction rate and low origination rate, such as at the end of the *lundgreni* Zone, they may be unavoidable.

In terms of palaeoenvironment, the presence of abundant benthos and bioturbation indicates that the environment was oxygenated during the *lundgreni* Zone. There is no evidence for environmental change at the end of the *lundgreni* Zone, although exposure was poor or non-existent at that horizon. This contrasts with the results from UK fieldwork (Chapter 3), in which the *lundgreni* Zone was anoxic, with environmental changes at the end of the zone. In contrast with other areas, there is no regression in Australia at the end of the *lundgreni* Zone (Talent 1989), which would account for the apparent lack of sedimentological change. The absence of regression is probably accounted for by the fact that there was active tectonism at the time, which would have had a stronger effect on local conditions than a global sea level change. This absence of regression may have something to do with Australia acting as a refugium – possibly conditions did not change as much as in other areas.

5. Homerian graptoloid faunas

This chapter is a summary of the current state of knowledge of Homerian graptoloid faunas worldwide. It provides background information for the dataset used in Chapter 6 and, in addition, details of faunas that were not included in the dataset. This is not intended to be a historical review of work on Homerian graptoloids, so most older literature has not been included. References to older literature can be found in the references mentioned here.

Homerian graptoloids are known from every continent, with the exception of Antarctica, but the faunas of some areas are better studied than those of others. The European faunas are best known, both because of the long history of graptolite research there and because Homerian graptoloids occur in many parts of the continent. In Africa, graptolites are known only from North Africa. Asian Homerian graptoloid faunas are found in central Asia, China, Malaysia and Siberia. In Australia, the area of interest is the southeast (New South Wales and Victoria). In the Americas, faunas have been identified in Canada, Alaska, Nevada, Bolivia and Argentina. These occurrences cover a reasonable palaeogeographic spread. There are some problems with sampling bias, out of date taxonomy and synonymy, discussed below (Section 5.1.3).

5.1 Background to the study

5.1.1 Description of search methods used

Lists of references were compiled using the electronic reference services Georefs and Geobase (http://firstsearch.uk.oclc.org/athens) and Web of Science (http://wos.mimas.ac.uk). Web of Science contains references from 1981, Geobase from 1980 and Georefs from 1785 for North America and 1933 for the rest of the world. Georefs was found to be the most useful, as it is a specifically geological database and hence contains many references not in the other two sources, and also goes back much further in time.

A list of approximately 1200 references in English, French, German, Polish, Russian, Chinese, Spanish, Portuguese, Italian and Romanian, was gathered of which several hundred were actually seen. (Some references were listed more than once, so the actual number of references gathered is lower than 1200.) References were included in the list if it seemed that they might mention graptoloids of *lundgreni, parvus-nassa* or *ludensis s.l.* Zone age. This resulted in many references being included that were not useful, but it was not possible to tell which these would be without seeing them. Most of the references looked at did not deal with graptoloids of the correct age. Sixty-three references have been included in the Chapter 6 dataset; some other references that included Homerian graptoloids were not included in the dataset but are mentioned below.

The information from the various references was recorded on forms, listing all the species present in each zone for each locality. This information was then used to draw up for each species a list of all the zones and the places that the species is found in. Records of "?" "cf." "sp." "aff." and "ex gr." have been included in the database and marked as such, as some morphological differences across the range of a species might be expected, particularly at the edges of a species' range. A list of all the references used for the dataset is given in Appendix 1.

5.1.2 Correlation of references with the global biozonal scheme

The zonal scheme of Koren' *et al.* (1996) was used (see Section 2.1 for details). The correlations of all the references used in the database with this scheme are given in Appendix 2. Where possible, the *ludensis* Zone *s.l.* was subdivided into the *praedeubeli-deubeli* and *ludensis s.s.* zones. This could not be done in many cases.

5.1.3 Taxonomic and sampling problems

5.1.3.1 Taxonomic problems

There are two taxonomic problems: firstly that the taxonomy in older references is out of date, and secondly, that some species may have been given different names by different workers.

Out-of-date taxonomy is a problem when dealing with older references, particularly where groups have been extensively revised. To avoid this problem, older references were not used where possible; in some areas, such as parts of the former Soviet Union, there are few recent studies and so details of faunas had to be taken from older literature.

The problem of out-of-date taxonomy applies especially to *Colonograptus ludensis*. The species that is now called *Colonograptus ludensis* has in the past also been called *Monograptus gotlandicus* and *Monograptus vulgaris* (Holland *et al.* 1969). Some of the specimens referred to *M. vulgaris* are what is now called *Pristiograptus jaegeri* (Holland *et al.* 1969). Thus references to *M. vulgaris* could refer to *C. ludensis* or *P. jaegeri*. The exception to this is Jaeger (e.g. 1991), who, because of a disagreement over who was the first reviser of *ludensis/vulgaris*, consistently used the species name *vulgaris* where other workers would have used *ludensis*. To summarise: pre-1969 records of *M. vulgaris* could be *C. ludensis* or *P. jaegeri*, and it is impossible to tell which species is present unless the specimens are illustrated or the material is re-examined. For this reason, references before 1969 have not been used wherever possible.

Species names have not been synonymised, as this was not possible for most species – many of the references used were compilation range charts, rather than taxonomic studies, and so did not have synonymy lists. The few cases where synonymy was possible are discussed separately below (*Monograptus digitatus* and *Pristiograptus etheringtoni* in sections 5.2.2.1 and 5.2.2.3 respectively). This problem is likely to have affected estimates of diversity – if one species has been given more than one name, species diversity will have been overestimated. Similarly, apparent endemism will be greater than actual endemism if the same species has been given different names in different areas.

Some of the species included in the dataset have been divided into subspecies, e.g. *Testograptus testis* has five subspecies (*T. t. bartoszycensis* Jawor., *T. t. disciformis* Bouček, *T. t. incomptus* Lenz & Melchin 1991, *T. t. inornatus* Elles 1900, *T. t. testis* (Barrande 1850)), as does *Monograptus flemingii* (*M. f. compactus* Elles & Wood 1913, *M. f. elegans* Elles in Boswell & Double 1940, *M. f. flemingii* (Salter 1852), *M. f. primus* Elles & Wood 1913, *M. f. warreni* Burns & Rickards 1993). Subspecies have not been included in the dataset, except in the few cases where only one subspecies was present in the data. This was because some authors gave identifications of graptoloids to the subspecific level, but most did not, so it was impossible to know what subspecies were present for most of the references in the dataset.

5.1.3.2 Sampling problems

The graptoloid faunas of some areas are better known than those of others, and monograptid faunas are better known than retiolitid faunas in almost all areas.

Some areas of the world have more records of graptoloid faunas than others. In particular, European faunas have been extremely well studied for over 150 years, (Section 5.2.1). Some areas have in reality few or no Homerian graptoloids, for example North America (Section 5.2.2) and southern Africa (Sections 5.2.4), but in other areas, such as South America, the apparent lack of graptoloid faunas could reflect a lack of exploration (Section 5.2.3). This Eurocentric bias means that studies of the *lundgreni* event will inevitably reflect what happens in Europe more than what happens in the rest of the world. Although the pattern of events during and after the extinction seen in Europe (Jaeger 1991) is similar to that seen in some other areas, such as Arctic Canada and central Asia (Koren' 1991; Lenz & Kozłowska-

Dawidziuk 2001a), this may not apply globally. For example, the survival of *Cyrtograptus* and *Monograptus s.s.* in Australia (Rickards *et al.* 1995a; Rickards & Wright 1997) indicates that the pattern of the event was different in this region. The lack of faunas from South America and Antarctica means that we have no idea what happened there at the end of the *lundgreni* Zone.

Retiolitids are subject to strong sampling bias, for two reasons. Firstly, they are difficult to see in the field (because their periderm is reduced to a meshwork) and hence subject to strong (unconscious) collector bias. They can also difficult to identify in non-isolated form (Lenz & Kozłowska-Dawidziuk 2001a, 2002b). These collection and identification problems mean that retiolitid faunas are more poorly known than monograptid faunas for most areas (Lenz & Kozłowska-Dawidziuk 2002b). Homerian isolated graptoloids are known in Poland and Arctic Canada, so the retiolitid faunas of these areas are the best known in the world. (Isolated graptoloids are also known from Sweden, e.g. the specimen of *Gothograptus nassa* illustrated in Rickards & Palmer 2002, but these have not received the same attention that Polish and Canadian faunas have.)

5.2 Background information on the data used in the study

The following section gives background information on the references used in the Chapter 6 database, and also instances of possible *lundgreni-ludensis* faunas where the biostratigraphic dating is not quite good enough to give a definite age. Areas where this is the case would be good places for further research on the *lundgreni* event. Where a reference is given a number, this refers to the list of references used for the dataset in Appendix 1.

5.2.1 Europe

Homerian graptoloids are known from Scotland (White *et al.* 1991), England (Holland *et al.* 1969; Rickards 1969), Ireland (Palmer 1970; Burns & Rickards 1993), Wales (Warren 1971; Zalasiewicz & Williams 1999), the Iberian peninsula

(Jaeger & Robardet 1979; Gutiérrez-Marco *et al.* 1996, 1997), Germany (Jaeger 1991), Italy (Barca & Jaeger 1989), Denmark (Bjerreskov & Jørgensen 1983), Poland (Teller 1969; Kozłowska-Dawidziuk 1990, 1995, 1999), the Czech Republic (Křiz *et al.* 1993; Štorch 1994a; Kozłowska-Dawidziuk *et al.* 2001), Romania (Iordan & Rickards 1970, 1974; Iordan 1981), Sweden (Jeppsson & Calner 2000), Bulgaria (Sachanski 1998) and the Baltic region (Paškevičius 1979; Kaljo *et al.* 1984). These are discussed below.

5.2.1.1 Possible *lundgreni, parvus-nassa* or *ludensis* Zone faunas

There are some faunas, discussed below, from the Isle of Man, Belgium and France that are probably of *lundgreni* Zone age, but have not been included in the database because of uncertainties in the dating and taxonomic difficulties, particularly with the older literature.

Howe (1999) described a graptolite fauna of probable *lundgreni* Zone age from the Niarbyl Formation, Isle of Man, UK. He listed *Cyrtograptus* cf. *lundgreni, Monograptus flemingii* cf. *warreni* Burns & Rickards 1993 and *Monograptus* ex. gr. *flemingii*. This fauna has not been included in the analysis, because of the uncertainties in the identifications of the species.

Verniers & Rickards (1978) reported some Wenlock graptolite assemblages from Belgium, including one containing *Monograptus flemingii, Cyrtograptus*? sp, *Monoclimacis ?flumendosae* and *Pristiograptus dubius*. This could be *lundgreni* age, but the species listed also occur in earlier biozones.

Philippot (1950) listed, but did not illustrate, *Monograptus vulgaris*, *M. flemingii* and *Cyrtograptus lundgreni* as being present in the Armorican Massif, France. The presence of *Cyrt. lundgreni* indicates the *lundgreni* Zone, and the occurrence of *M. flemingii* is consistent with this. *M. vulgaris* (which could be C. *ludensis* and/or *P. jaegeri* in modern taxonomic terms) indicates the presence of the *ludensis* Zone *s.l.* As Philippot did not illustrate *M. vulgaris*, it is not possible to tell which species it is.

5.2.1.2 Western Europe

Homerian faunas are known in many areas of mainland Britain. In England, *lundgreni* to *ludensis* Zone graptoloids occur in northern England (Rickards 1965, 1969, reference 50) and Shropshire (Holland *et al.* 1969, reference 46). Graptoloids are found in the *lundgreni* Zone graptoloids in the south of Scotland, but the top of the zone is not seen (White *et al.* 1991, reference 47). In Wales, *lundgreni* to *ludensis* Zone faunas occur in North Wales (Warren 1971, reference 45), central Wales (Zalasiewicz & Williams 1999, reference 43) and the Welsh Borderland (Elles 1900; Wood 1900; Das Gupta 1932; Palmer 1972; Chapter 3 of this thesis).

The Republic of Ireland has *lundgreni* and *ludensis* Zone faunas (e.g. Palmer 1970, reference 60; Burns & Rickards 1993, reference 51).

The best-preserved and most diverse graptoloid faunas in Germany are those of Thuringia (Maletz 2001). Jaeger (1991, reference 35) provided an extremely detailed zonal sequence for the Homerian of this region, dividing the *lundgreni-ludensis* interval into six zones. The zones and their correlation with the standard sequence are given in Appendix 2.

Jaeger & Robardet (1979, reference 37) illustrated a number of sections from the Ossa Morena Zone of southern Spain showing exact occurrences of graptoloids and a composite section showing which zones were present in the area. Gutiérrez-Marco *et al.* (1996, reference 34) restudied one of Jaeger & Robardet's sections and, in addition, worked on two sections in the Barrancos area, Portugal. Both of these references contain *lundgreni, parvus-nassa* and *ludensis* Zone faunas. The assemblage listed by Gutiérrez-Marco *et al.* (1997, reference 36) is *lundgreni* Zone, and was identified by the authors as such on the basis of the occurrence of *Cyrtograptus hamatus*.

The graptoloids of Sardinia were studied by Meneghini (1857), and later by Gortani (1923a, b). In recent years they have been looked at by Jaeger (1976), Barca & Jaeger (1989, reference 49) and Rickards *et al.* (1995b).

In Scandinavia, Homerian graptoloids are not common. Bjerreskov & Jørgensen (1983, reference 38) described a *lundgreni* Zone fauna from Bornholm. They thought that the record was lower *lundgreni* Zone. Jeppsson & Calner (2000, reference 61) gave graptoloid species ranges for a composite section through the *lundgreni, parvus-nassa* and *praedeubeli-deubeli* zones on Gotland. Their zonation was more finely divided than in many areas, with two zones in the *parvus-nassa* interval and recognition of separate *praedeubeli* and *deubeli* zones.

5.2.1.3 Eastern Europe

The graptolite succession of the Czech Republic has been studied by many workers from Barrande (1850) onwards. In this study only the most recent references have been used, because of taxonomic differences between older and more recent works. Štorch (1994, reference 41) provided a compilation of the graptolite succession of Bohemia up to the top of the *ludensis* Zone, including information from the Všeradice section. The Všeradice section is the only one in the Barrandian area that spans the *lundgreni, nassa* and *ludensis* zones (Chlupáč *et al.* 1998). For this section, Křiz *et al.* (1993, reference 33) studied the *lundgreni* Zone graptolites, and Kozłowska-Dawidziuk *et al.* (2001, reference 32) the *parvus-nassa* to *nilssoni* zones.

Iordan (1981, reference 59) studied the Silurian and Devonian faunas of the Moesian Platform, southeastern Romania. The study was done from borehole sections, as most of the Palaeozoic of the Moesian Platform is only present in the subsurface (Iordan 1981). She identified the *lundgreni, testis* and *nassa-vulgaris* zones as occurring in the Moesian platform. The *lundgreni* and *testis* zones are correlated with the *lundgreni* Zone of this study, and the *nassa-vulgaris* Zone with the *parvus-nassa* and *ludensis* zones.

Poland is one of the three places where isolatable retiolitids are known in the Homerian, the others being Arctic Canada and Sweden. This means that the retiolitids of Poland are known in much more detail than that of most other places, particularly because of the recent work of Anna Kozłowska-Dawidziuk (1990, 1995, 1997, 2001, 2002). A great deal of the work done has been from borehole material, as much of the Polish Silurian is in the subsurface.

Teller (1969, reference 40) summarised the Silurian graptolite biostratigraphy of Poland. This reference has been included because it is the only source dealing with the whole of Poland, although some of the taxonomy is now slightly out-of-date (for example, the species *Monograptus vulgaris* is listed as being present – see section 5.1.3.1).

The other Polish references deal with isolated material from single cores. Kozłowska-Dawidziuk (1990, reference 62, 1995, reference 63) described many species of retiolitids, including new species, from isolated material from the Zawada 1 borehole, northeast Poland. These two references deal with the *lundgreni* Zone only. Kozłowska-Dawidziuk (1999, reference 20) illustrates species from the *lundgreni*, *parvus-nassa* and *praedeubeli* zones of the Bartoszyce IG 1 borehole of northeast Poland.

Paškevičius (1979, reference 44) summarised the graptolite succession of Lithuania and distinguished the *Monograptus testis* Zone (divided into the *Monograptus testis* and *Gothograptus tenuis* subzones), the *Gothograptus nassa* Zone and the *Monograptus ludensis* Zone. Paškevičius drew the base of the *testis* Zone at the first appearance of *M. testis*. *Cyrtograptus lundgreni* is also present in Lithuania, but appears earlier than *M. testis*, so that *Cyrt. lundgreni* appears in the *Cyrtograptus radians* Zone (*radians* being the zone below *testis*). Data from the *radians* zone has not been included in the dataset. Kaljo *et al.* (1984, reference 3) summarised graptoloid data from Estonia, Latvia and Lithuania.

Graptolite-bearing sediments occur in the west of Bulgaria (Sachanski 1998, reference 53). Sachanski (1998) summarised the known occurrences of Silurian and Devonian graptolites in Bulgaria. He identified the *Cyrtograptus lundgreni* and *Colonograptus ludensis* zones, but not the *parvus-nassa* Zone.

5.2.2 North America

Homerian graptoloids are known from Alaska (Churkin & Carter 1996), Nevada (Berry & Murphy 1975; Mullens 1980), Arctic Canada (Thorsteinsson 1958; Lenz 1978a, 1990, 1993b, 1993c, 1994d, 1994e, 1994a, 1994c, 1995; Lenz & Melchin 1987, 1990, 1991; Lenz & Kozłowska-Dawidziuk 2001a, 2002a), the Northwest Territories (Lenz 1980, 1988), Quebec (Bourque & Lachambre 1980) and North Greenland (Bjerreskov 1986, 1992).

5.2.2.1 USA

Faunas that may belong to the Homerian occur in New York, Washington state, Idaho and Maine. Definite Homerian faunas are known from Nevada and Alaska.

Berry & Boucot (1970) reported that a possible *Gothograptus nassa* had been found in the Lockport Group of New York. *G. nassa* occurs in the *lundgreni, nassa-dubius* and *ludensis* zones.

A fauna containing *Monograptus flemingii* and *Monoclimacis flumendosae* is known from Washington state (Greenman *et al.* 1977). This assemblage could be *lundgreni* Zone but as these species occur below as well as in the *lundgreni* Zone (Rickards 1976) this record has not been included in this study.

Wenlock graptolites have been found in Idaho. A stratigraphically lower collection contains graptolites identified as *Monograptus flemingii*? and *Cyrtograptus perneri*?, and a collection above this contains *Monograptus flemingii*? and a possible monoclimacid (Dover & Ross 1975). *Cyrtograptus perneri* is the zonal fossil for the *perneri* Zone, which is below the *lundgreni* Zone. The upper collection could be *lundgreni* Zone age, but without a zonal fossil (*Cyrtograptus lundgreni* or *Testograptus testis*) it is not possible to tell.

Pavlides & Berry (1966) described finds of graptolites of late Wenlock age from Aroostook County, Maine. The graptolites could not be assigned to a definite zone, because the cyrtograptids were poorly preserved. One assemblage included a cyrtograptid that could be *Cyrtograptus lundgreni* and a poorly preserved monograptid similar to *Testograptus testis inornatus* (Pavlides & Berry 1966). This assemblage would be *lundgreni* Zone if the graptoloids are *Cyrt. lundgreni* and *T. testis*, but Pavlides & Berry (1966) did not assign it to any particular zone.

Berry & Murphy (1975, reference 14) studied several sections in the Roberts Mountains Formation, central Nevada. They defined a zonal scheme including the *Testograptus testis, Pristiograptus dubius frequens* and *Pristiograptus ludensis* zones.

The *Pristiograptus dubius frequens* Zone is correlated with the *parvus-nassa* Zone in the global scheme (Koren' *et al.* 1996) because its base, defined as the first appearance of *Pristiograptus dubius frequens*, is at approximately the level where *Testograptus testis*, *Monograptus flemingii*, *Monoclimacis flumendosae* and *Cyrtograptus* disappear (Berry & Murphy 1975). The diversity at this locality is somewhat higher than in some areas, consisting of at least five species (*P. dubius frequens, P.* cf. *P. praedubius*, *Gothograptus nassa, Spinograptus spinosus* and holoretiolitids).

Mullens (1980) also reported *testis* Zone and *dubius-nassa* Zone graptolites from the Roberts Mountains Formation, but as all the species he mentions were listed by Berry & Murphy (1975), his data have not been included.

Churkin & Carter (1996, reference 1) mapped an area of Ordovician-Silurian graptolite-bearing rocks in the Terra Cotta Mountains, Alaska Range. They identified the Terra Cotta Mountains Sandstone as containing the *Cyrtograptus centrifugus, Cyrtograptus lundgreni*, *Monograptus digitatus* and *Monograptus ludensis* zones. They correlated their *M. digitatus* Zone with the *Gothograptus nassa* Zone of the British sequence, and their *M. ludensis* Zone with the British *M. ludensis* Zone, i.e. the *ludensis* Zone *s.l.* However, *Monograptus digitatus* is a junior synonym of *Lobograptus? claudiae* (Lenz & Kozłowska-Dawidziuk 2002a). This species is otherwise known from the *praedeubeli-deubeli* Zone of Arctic Canada (Lenz & Kozłowska-Dawidziuk 2002a) and the equivalent zone in central Asia (Koren' 1992). Therefore, I correlate the *M. digitatus* plus the *M. ludensis* zones with the *ludensis* Zone *s.l.*

5.2.2.2 Greenland

Graptoloids are known only from North Greenland. The graptolite zones are similar to those of Arctic Canada (Bjerreskov 1992, reference 13), although the *parvus-nassa* and *ludensis* zones have not yet been reported from Greenland. Bjerreskov (1992) recorded *lundgreni-testis* Zone graptolites from the Peary Land Group, identified from the presence of *Testograptus testis*.

There are some other graptolite occurrences in North Greenland that may be from the *lundgreni* Zone. *Monograptus flemingii* and the dendroid *Callograptus pulchellus* are known from Washington Land (Bjerreskov 1981, 1986). The presence of *M. flemingii* could indicate the *lundgreni* Zone, but the species also occurs in earlier zones. Bjerreskov (1986) noted that *Cyrtograptus* aff. *C. mancki* had been found in Nyboe Land. *C. mancki* occurs in the *lundgreni* Zone in Arctic Canada (Lenz 1978). This record has not been included in the analysis, because the *lundgreni* biozone cannot be definitely identified from the presence of *C.* aff. *C. mancki*.

5.2.2.3 Canada

The Cape Phillips Formation of the Canadian Arctic Archipelago contains Wenlock and Ludlow strata. Wenlock graptolites were first reported from the Cape Phillips

Formation by Thorsteinsson (1958, reference 12). Graptolites are found both in flattened and in isolatable form, in nodules. This is one of only two places in the world, the other being Poland, where isolatable Homerian graptoloids are known to occur. Isolated retiolitids have been described by Lenz (1993b, reference 6, 1993c, 1994d, 1994c, reference 5), Lenz & Kozłowska-Dawidziuk (2001a, reference 2, 2002a, reference 52) and Lenz & Melchin (1987). Isolated monograptids and cyrtograptids have been described by Lenz (1978, 1990, 1994a), and flattened monograptids and cyrtograptids by Lenz (1994e, 1995, reference 4) and Lenz & Melchin (1991, reference 8).

The biozonal scheme for the Cape Phillips Formation has been revised extensively in recent years. As recently as 1990, Lenz & Melchin used a scheme that recognized only the *lundgreni-testis* and *ludensis* zones. At that time there was not enough information to recognise the *parvus-nassa* and *praedeubeli-deubeli* zones. Lenz (1995) produced a refined scheme that included the *dubius*-"*nassa*" (equivalent to *parvus-nassa*), *praedeubeli-deubeli* and *ludensis* zones. This scheme has been used in the most recent publications.

For some references on the Cape Phillips Formation only some of the information given has been used, where better information is given in another paper. For Lenz 1993b (reference 6) I have only used information from the *lundgreni* Zone, as the "*ludensis*" Zone graptolites were dealt with in more detail in Lenz (1995). For Thorsteinsson (1958) only data from the type section (his Locality 19) has been used, as the other sections in his paper are dealt with in more detail by Lenz.

Lenz (1980, reference 10; 1988, reference 9) described *lundgreni* Zone graptoloids from two close localities in the Northwest Territories. The correlation of the fauna of Lenz (1988) with the *lundgreni* Zone is straightforward; that of Lenz (1980) is somewhat less so.

The zonal sequence given in Lenz (1980) for a twenty metre section at Clearwater Creek is as follows (youngest first):

"Beds with *Pristiograptus etheringtoni*"
testis-lundgreni Zone
"Beds with *Monograptus firmus nahanniensis*"
rigidus Zone
"Beds with *Cyrtograptus* cf. *perneri*"
centrifugus Zone

The parts of this sequence that are of interest for this study are the two upper divisions. The "beds with *Monograptus firmus nahanniensis*" have not been included in the analysis, because if they are *lundgreni* Zone, they are the lower part of it.

The correlation of the *etheringtoni* beds is somewhat problematic. Lenz (1980) said that the age of the beds is "equivocal," and that they were probably equivalent to the *nassa-dubius* or *ludensis s.l.* zones. Lenz & Melchin (1991) correlated the *etheringtoni* beds with the *nassa* and *ludensis* zones of Rickards (1976). As *P. etheringtoni* is a junior synonym of *Lobograptus? sherrardae* (Lenz & Melchin 1991), this is a sensible correlation. (*L*? *sherrardae* is a zonal fossil for the *sherrardae* subzone, equivalent to the lower part of the *praedeubeli-deubeli* Zone.) However, *Cyrtograptus lundgreni*, the index fossil for the *lundgreni* Zone, is also found in the *etheringtoni* beds. The other fossils in the beds (?*Gothograptus* sp. and *Pristiograptus dubius*) are of no use for dating. As *P. etheringtoni* also occurs in the *lundgreni* Zone (Lenz 1980), the "beds with *Pristiograptus etheringtoni*" have been included in the database in the *lundgreni* Zone.

Bourque & Lachambre (1980, reference 11) mention an occurrence of *Colonograptus ludensis* on the Gaspé Peninsula, Quebec. This reference has been included because it is the only record of Homerian graptoloids in Quebec that I have been able to find.

5.2.3 South America

Silurian rocks are found in Argentina, Bolivia, Brazil, Paraguay, Peru and Venezuela (Berry & Boucot 1972b), with Silurian graptolites being known from Argentina

(Cuerda 1965, 1969; Amos 1972; Peralta 1985; Cingolani *et al.* 1992; Rickards *et al.* 1996; Rubinstein & Brussa 1999), Bolivia (Branisa *et al.* 1972; Cuerda 1974; Toro *et al.* 1998; Maletz *et al.* 2002), Brazil (Lange 1972) and Paraguay (Harrington 1950, 1972). Some of these occurrences are lower Ludlow (e.g. Cuerda 1969, 1974; Peralta 1985), and two are Late Wenlock (Cingolani *et al.* 1992; Maletz *et al.* 2002). Both the Late Wenlock references are discussed separately below.

Cingolani *et al.* (1992) report that *Pristiograptus dubius*, *P. jaegeri*, *Monograptus argentinus* and *Retiolites* sp. are found in the Lipeon Formation, northeastern Argentina. I find it difficult to assign this to a zone. *P. dubius* is long-ranging and so useless for dating, and *P. jaegeri* is found in both the *lundgreni* Zone and the *ludensis* Zone *s.l.* *M. argentinus* is a Lower Ludlow species (Cuerda 1969). Thus it appears that the Lipeon Formation is Late Wenlock to Ludlow in age. This record does show, based on the occurrence of *P. jaegeri*, that Late Wenlock graptolite-bearing rocks are present in Argentina. This might be a fruitful area for more research.

Maletz *et al.* (2002, reference 42) mention that *Colonograptus praedeubeli* occurs at the base of the Kirusillas Formation of Bolivia. This is the same occurrence mentioned by Jaeger (1991). Maletz *et al.* (2002) gave the age of this occurrence as Late Homerian, which is *ludensis* Zone *s.l.* in the terminology of this study. The discovery of other graptoloids in the same beds would allow more precise dating.

The apparent lack of South American Homerian graptoloids may be at least partly due to the rocks being less well known than on other continents, for example, the Silurian was not recognised in Venezuela until 1964 (Boucot 1972). The other possibility is that there are in reality very few graptoloids there. South America was at high latitude during the Late Wenlock, so it is possible that few graptoloids could live there.

5.2.4 Africa

Graptolite faunas of Wenlock age are known from North Africa. Graptolites appear to be entirely absent from southern Africa (Boucot 1999); the furthest south that graptolites are known is Guinea, but these are of Llandovery age (Konde 1981).

In North Africa, graptolites of *lundgreni* to *ludensis* age are known from Morocco (Willefert 1966; Bohrman & Fischer 1985; Destombes *et al.* 1985; Cornée *et al.* 1987; Lüning *et al.* 2000), Algeria (Massa 1965), Tunisia (Jaeger *et al.* 1975) and Libya (Massa & Jaeger 1971). Homerian graptolites may be present in Mauritania (Deynoux *et al.* 1985 p.375), western Libya (Massa & Jaeger 1971) and Senegal (Deynoux *et al.* 1985 p.400).

In the Mauritanian Adrar, *Cyrtograptus lundgreni* and *Cyrt. ellesi* [sic] are possibly present in the Oued Chig Formation (Deynoux *et al.* 1985 p.375). If present, these species would indicate the *lundgreni* Zone.

Massa & Jaeger (1971) found an association of *Gothograptus nassa* and *Pristiograptus* cf. *dubius* in the Rhadames Basin, western Libya. They said that this was the Wenlock-Ludlow boundary. As defined then, the Wenlock-Ludlow boundary was at the base of the *ludensis* Zone *s.l.*, so this occurrence could represent the *parvus-nassa* Zone. However, as both species occur before and after this zone it is not possible to be sure of the age, and so this reference has not been included in the dataset.

Monograptus vulgaris Wood 1900 reportedly occurs in the Kolda boring, southern Senegal (Deynoux *et al.* 1985 p.400). This record has not been included in the dataset, as it is not clear which species is meant. *Monograptus vulgaris* is, in modern taxonomic terms, either *Colonograptus ludensis* or *Pristiograptus jaegeri* (see section 5.1.3.1). This record probably indicates the *ludensis* Zone *s.l.*

Massa (1965, reference 21) mentioned a *lundgreni* Zone assemblage from the Ben Zireg area, Algeria. *Colonograptus deubeli* is also present, indicating the *ludensis* Zone *s.l.* She did not provide any illustrations of the graptoloids. The same assemblage is mentioned by Jaeger & Massa (1965).

In Morocco, graptolites are known from the *lundgreni* Zone (Willefert 1966, reference 18) and the *ludensis* Zone *s.l.* (Bohrman & Fischer 1985, reference 15; Cornée *et al.* 1987, reference 16; Lüning *et al.* 2000, reference 19). Destombes *et al.* (1985) gave species lists for many places in Morocco, including unpublished assemblages and revisions of previously published material, but unfortunately did not distinguish zones in enough detail to be used in this analysis.

Willefert (1966) mentions that *Monograptus vulgaris* occurs at various sites in Morocco. This record of *M. vulgaris* could represent *Colonograptus ludensis* or *Pristiograptus jaegeri* (see Section 5.1.3.1). *C. ludensis* and *P. jaegeri* both occur in Morocco (Bohrmann & Fischer 1985; Cornée *et al.* 1987). Willefert did not illustrate the specimens in question, so it is not possible to tell whether they are *C. ludensis*, *P. jaegeri* or both. For this reason this record has not been included, although data on the *lundgreni* Zone from this reference has.

Jaeger *et al.* (1975, reference 17) described *lundgreni-ludensis* graptolites from the Tunisia-Libya border. They identified the *lundgreni* and *vulgaris* (= *ludensis s.l.*) zones, and also a bed between the two zones containing abundant *Pristiograptus dubius* and *Gothograptus nassa*. I correlate these beds with the *parvus-nassa* Zone.

5.2.5 Asia

Homerian graptoloids have not been reported from large parts of Asia. Faunas are known from Turkey (Dean *et al.* 1999), the Malay Peninsula (Jones 1973), China (Fu 1980; Lenz *et al.* 1996; Ni 1997; Zhang & Lenz 1997) and the former Soviet Union (Obut *et al.* 1965, 1967; Obut & Sobolevskaya 1966; Sobolevskaya 1976; Rinenberg 1990; Koren' 1991, 1992; Koren' & Suyarkova 1994; Koren' & Sobolevskaya 1998;

Paalits *et al.* 1998). Possible Homerian faunas occur in southeastern Turkey (Berry & Boucot 1972c), China (Ni & Song 2002) and Mongolia (Rutkowski & Słowański 1970).

Berry & Boucot (1972c) mention that *Pristiograptus dubius* and *Monograptus* cf. *M. flemingii* occur in the Hardof Formation, southeastern Turkey. This assemblage could be *lundgreni* Zone or a lower zone.

Rutkowski & Słowański (1970) reported the presence of *Testograptus* ex gr. *testis* and *Monograptus* cf. *flemingii* from "Kobdo aymak, the axial part of the Mongolian Altay, in the neighbourhood of the source of the seasonal Ulan-Gol stream which is a left tributary of the Kboytu-Tsenkhen-Gol Stream." This assemblage is also mentioned by Tomczykowa & Tomczyk (1970). This assemblage is probably *lundgreni* Zone, but has not been included as the presence of one of the zonal species is not definite.

Dean *et al.* (1999, reference 26) reported the presence of *Monograptus flemingii warreni* Burns & Rickards 1993 from southwestern Turkey. This species occurs in the upper part of the *lundgreni* biozone (Dean *et al.* 1999). *Monograptus flemingii* and *Pristiograptus dubius* also occur in the area, but not at the same locality as *M. flemingii warreni*. Although this reference only mentions one species, it has been included as it is the only definite reference to a *lundgreni* Zone fauna found.

Jones (1973, reference 25) reported the presence of the *Cyrtograptus lundgreni* Biozone from a single locality in central Kedah, Malay Peninsula. However, the only species present is the eponymous zonal fossil, so the dating must be regarded with due caution – zones should ideally be identified from the presence of many species. The record has been included in the database because it is the only occurrence of Homerian graptoloids in that part of the world. Jones also reported an assemblage of *Monograptus flexilis* Zone age from two localities in central Kedah, containing among other species *Monograptus flemingii*, *Monoclimacis flumendosae* and

Pristiograptus cf. *meneghini*. This proves that these species do occur on the Malay Peninsula. Further work is needed on faunas from this area.

Chen (1984) reviewed the occurrences of Silurian graptolite zones in China. He reported that the *lundgreni* Zone had only been recognised in Ziyang, southern Shaanxi by Fu (1980, reference 48). Chen (1984) recognised three zones above the *lundgreni* Zone, the *nilssoni*, *tumescens* and *transgrediens* zones. Thus, in 1984, the *ludensis* Zone was not known from China. Since 1984 the *ludensis* Zone *s.l.* has been recognised by several workers in Guangxi (Lenz *et al.* 1996, reference 28) and Yunnan (Ni 1997, reference 39; Zhang & Lenz 1997, reference 27). The *ludensis* zone *s.l.* may also be present in Shaanxi and Inner Mongolia (Ni & Song 2002).

Homerian graptoloid assemblages are known from many parts of the former Soviet Union. The sequences in Central Asia (Koren' 1991, reference 29; 1992, reference 57; Koren' & Suyarkova 1994, reference 30; Obut & Sobolevskaya 1966, reference 55; Rinenberg 1990, reference 58) span the *lundgreni*, *parvus-nassa* and *ludensis* zones. *Lundgreni* and *ludensis s.l.* Zone graptoloids occur in Taimyr, northern Siberia (Obut *et al.* 1965, reference 54), and *lundgreni* Zone faunas in the Kolyma Massif, northeastern USSR (Obut *et al.* 1967, reference 56). Some graptoloids also occur in the Urals, e.g. the *ludensis* Zone *s.l.* fauna described by Paalits *et al.* (1998, reference 31).

Paalits *et al.* (1998, reference 31) described *Colonograptus praedeubeli* from the Sermenovo Quarry, southern Urals. Unfortunately the only other graptoloids found were fragments of plectograptids, so assigning the occurrence a definite zonal position is difficult. The authors ascribed the occurrence to the *praedeubeli-deubeli* Zone of Koren' *et al.* (1996). However, *C. praedeubeli* also occurs in the *ludensis* Zone *s.s.*, therefore this occurrence can only be ascribed to the *ludensis* Zone *s.l.*

Homerian graptoloids also occur in the Novosibirsk Islands, northern Siberia, but no assemblages from there have been included in the dataset. Sobolevskaya (1976) mentioned a *Monograptus testis-Cyrtograptus lundgreni* Zone fauna of *Testograptus* aff. *testis*, *Monograptus nganasanicus*, *M.* ex. gr. *mutuliferus* Meneghini, *Colonograptus deubeli* and *Plectograptus* sp. from Kotelnyi Island. This assemblage appears to mix *lundgreni* Zone (*T.* aff. *testis, M. nganasanicus*) and post-*lundgreni* faunas (*C. deubeli*). Koren' & Sobolevskaya (1998) stated that it is possible to recognise the *testis*, *praedeubeli*, *sherrardae*, *deubeli* and *ludensis* zones on Kotelnyi Island. However, as this was an abstract, a full faunal list was not given, and so this reference has not been included.

5.2.6 Australia

As recently as 1922, Süssmilch (1922 p.46) was able to say "Graptolites, which occupied such a predominating position in Ordovician times, are not found. This group apparently became extinct in Australia at the close of the Ordovician." Since then Silurian graptolites have been described by Sherrard (e.g. 1954) and others, and more recently by Rickards and co-workers. Homerian graptolites are known from New South Wales (Rickards *et al.* 1995a, reference 22; Rickards & Wright 1997a, reference 23) and Victoria (Rickards & Sandford 1998, reference 24).

Australia is a refugium for graptoloids during the *lundgreni* event (Rickards & Wright 2002), so Australian faunas are particularly significant for the study of the event. *Monoclimacis* and *Cyrtograptus* are known from Quarry Creek, New South Wales (Rickards *et al.* 1995a), and there are several records of *Monograptus sensu stricto* occurring after the *lundgreni* Zone (Jenkins 1978; Rickards *et al.* 1995a; Rickards & Wright 1997). *Testograptus testis* survives the event in New South Wales (Rickards *et al.* 1995a) and possibly in Victoria (Rickards & Sandford 1998).

5.3 Discussion and conclusions

Homerian graptoloids are known from most areas of the world, but there are some gaps in the distribution. The faunas have been studied more extensively in some places, particularly Europe, than others. Areas that it would be most useful to find further occurrences of Homerian graptoloids in are: Australia, because of its role as a refugium, and South America and southern Africa, because these areas were at high latitude and so might have different faunas and/or patterns of extinction. The faunas of North Africa, Malaysia and China are poorly known or have not been studied in detail recently, and so would be good places for further research on the *lundgreni* event.

Some of the occurrences of Homerian graptoloids listed here cannot always be accurately located in the zonal sequence, for example the Argentinian record of *Colonograptus praedeubeli* described by Maletz *et al.* (2002) and the occurrence of *Cyrtograptus lundgreni* in Malaysia (Jones 1973). The possibility exists that these records represent post-extinction survival or early appearance, but is it impossible to know this without the presence of other biostratigraphically useful species.

6. Global database of late Wenlock species occurrences

This chapter deals with a global database of graptoloid species occurrences during the *lundgreni*, *parvus-nassa* and *ludensis s.l.* zones. A database of this type provides data that can be analysed statistically in order to test hypotheses about the causes of species extinction, such as that the geographical area occupied by a species affects its extinction probability. The results of studies on sections from a small region are obviously unsuitable for testing this hypothesis – this type of hypothesis can only be investigated using compilations of data.

Several hypotheses of the reasons for species extinctions are addressed: that extinction is random; that extinction probability is negatively correlated with geographical extent; that there are latitudinal variations in extinction patterns; that rare species are more likely to become extinct than common species and that K-selected species were more likely to become extinct than r-selected ones. The statistical methods used in this chapter are all described in Bailey (1959).

6.1 Results

Tables of species occurring in the *lundgreni*, *parvus-nassa*, *ludensis s.l.*, *praedeubeli-deubeli* and *ludensis s.s.* zones are given in Appendix 3. Figures 6.1 to 6.12 are maps of the localities for each zone for the present-day world and for the world in the Silurian. Despite the lack of graptoloid faunas in some areas, geographic coverage is reasonable. The only areas in the Silurian that are not covered are the far north, where no rock is known, and the southern high latitudes (present-day southern Africa and South America). Table 6.1 summarises the number of species present in each zone for each graptoloid subfamily.

The diversity in the *lundgreni* Zone is seventy-six species at forty-nine localities. The highest diversity at any one locality is twenty-five species at Locality 2 (Arctic Canada).

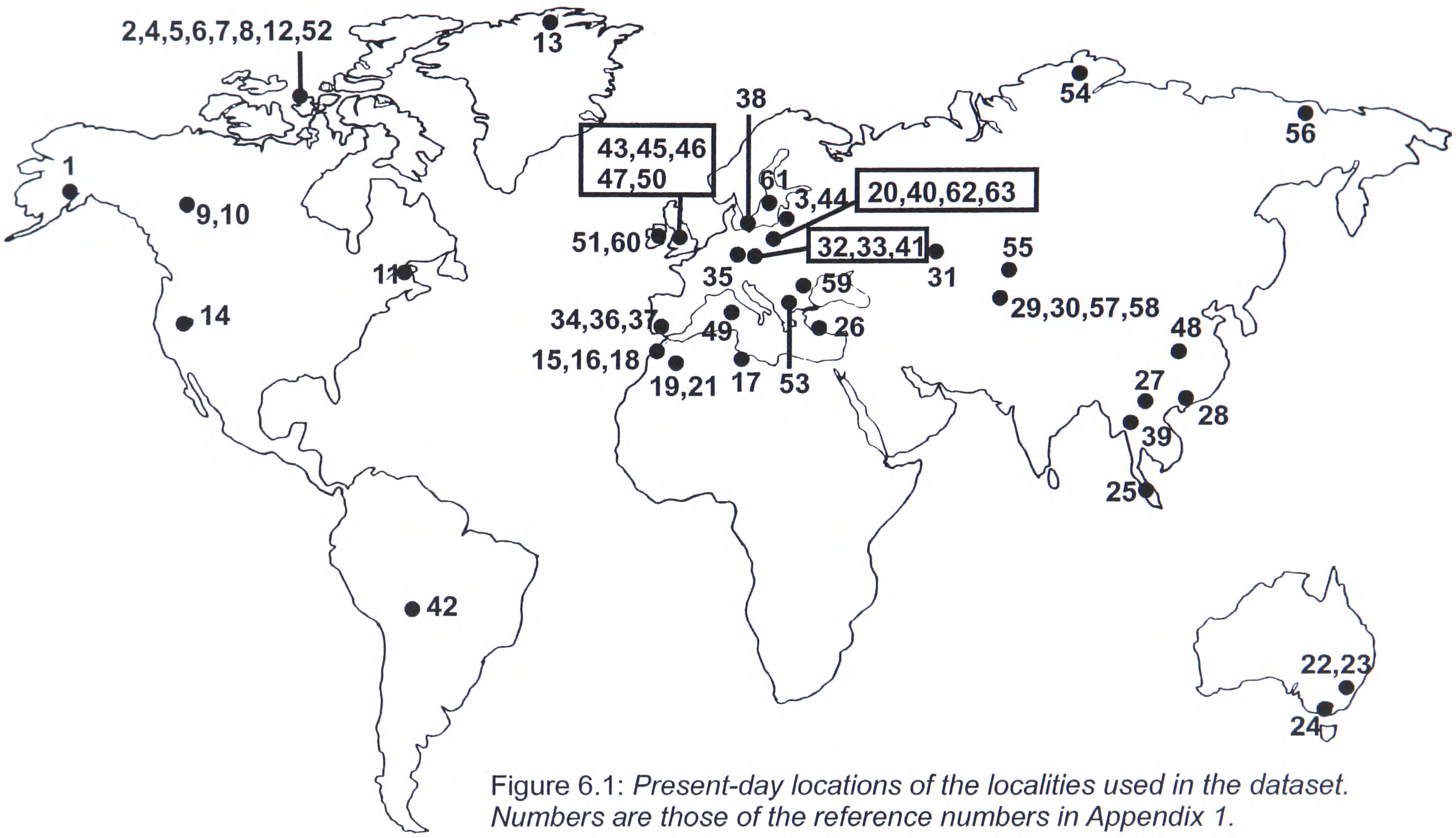


Figure 6.1: *Present-day locations of the localities used in the dataset. Numbers are those of the reference numbers in Appendix 1.*

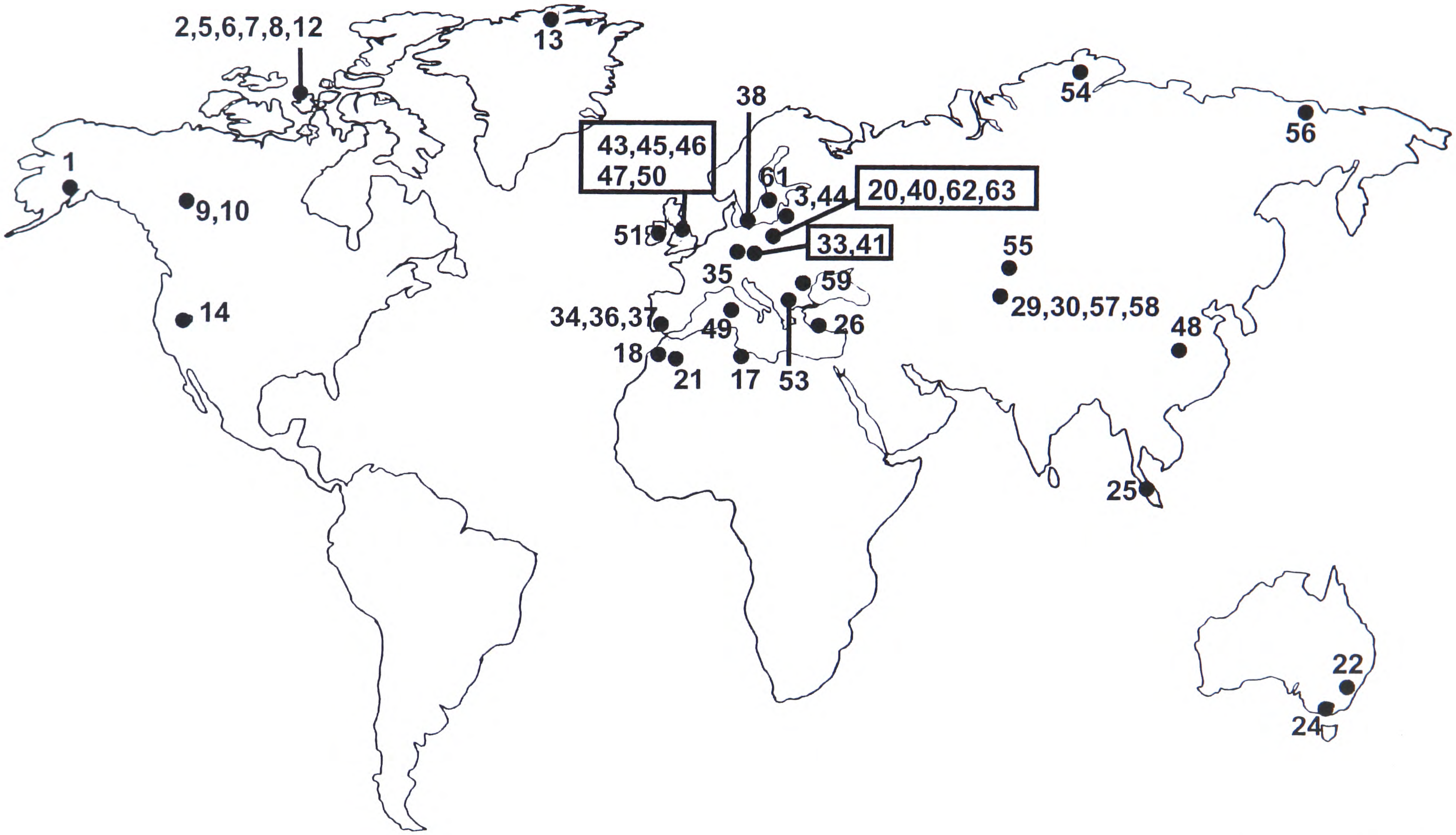


Figure 6.2: *Present-day locations of the* lundgreni *Zone localities used in the dataset. Numbers are those of the reference numbers in Appendix 1.*

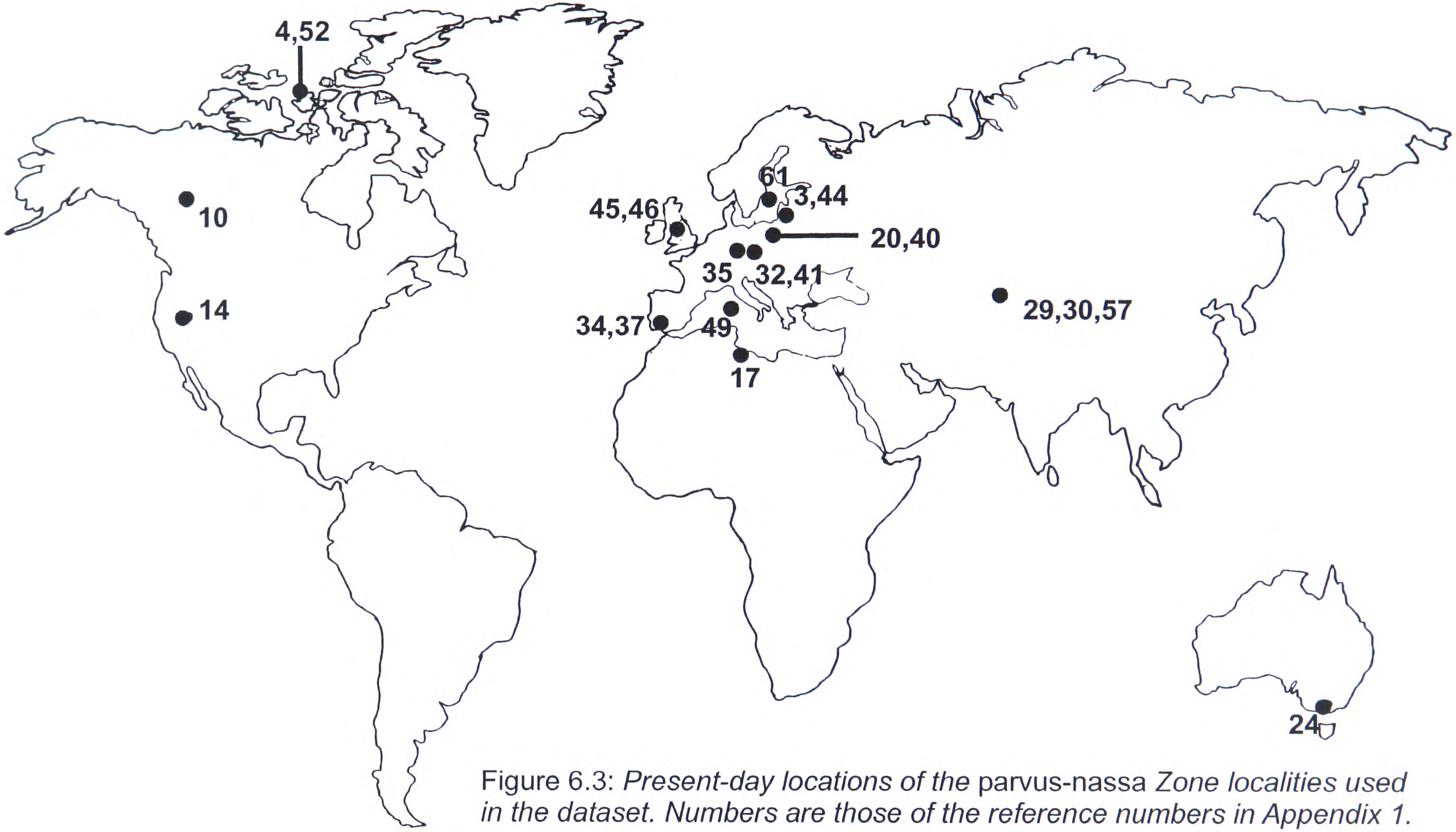


Figure 6.3: *Present-day locations of the* parvus-nassa *Zone localities used in the dataset. Numbers are those of the reference numbers in Appendix 1.*

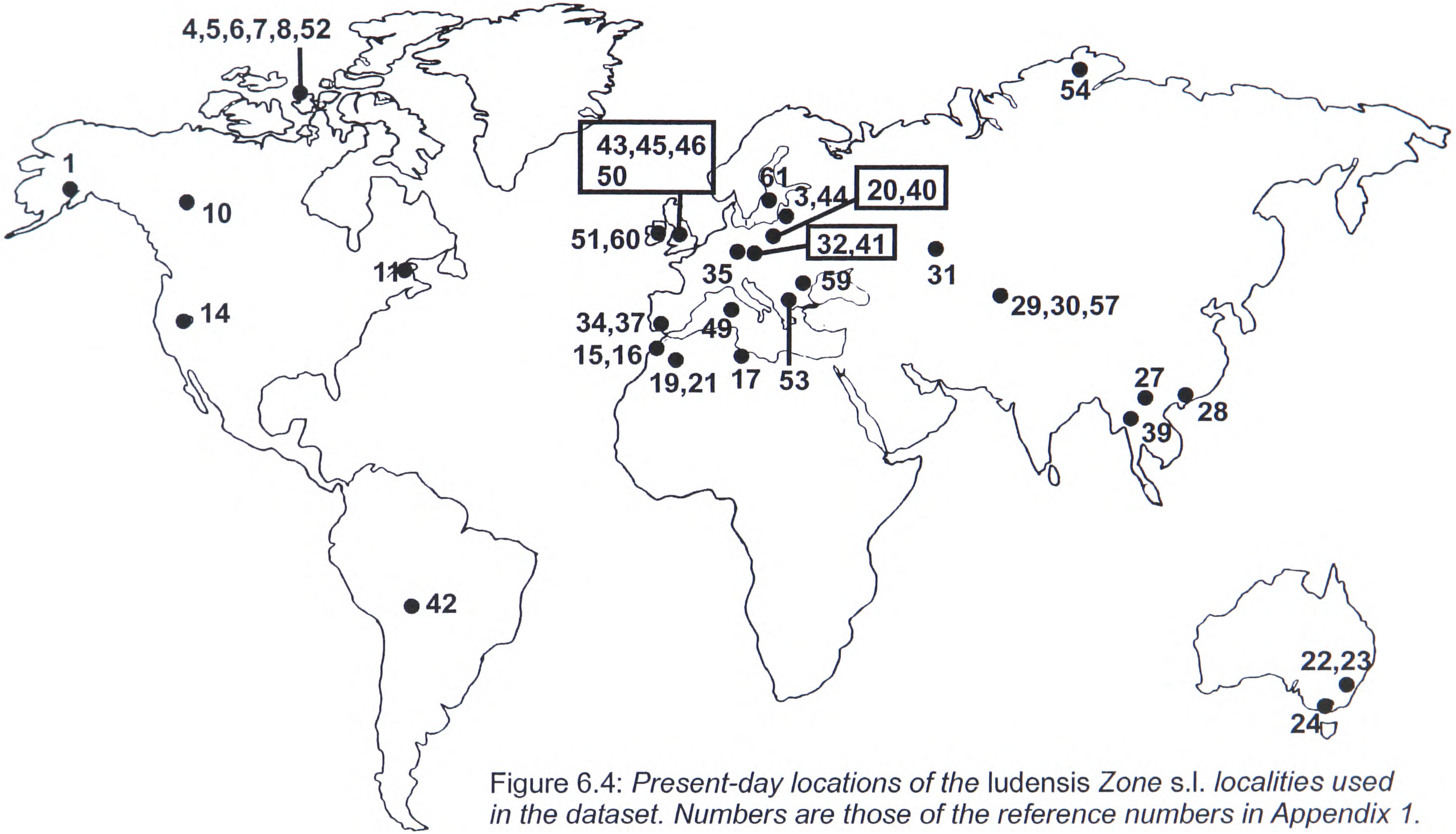


Figure 6.4: *Present-day locations of the* ludensis *Zone* s.l. *localities used in the dataset. Numbers are those of the reference numbers in Appendix 1.*

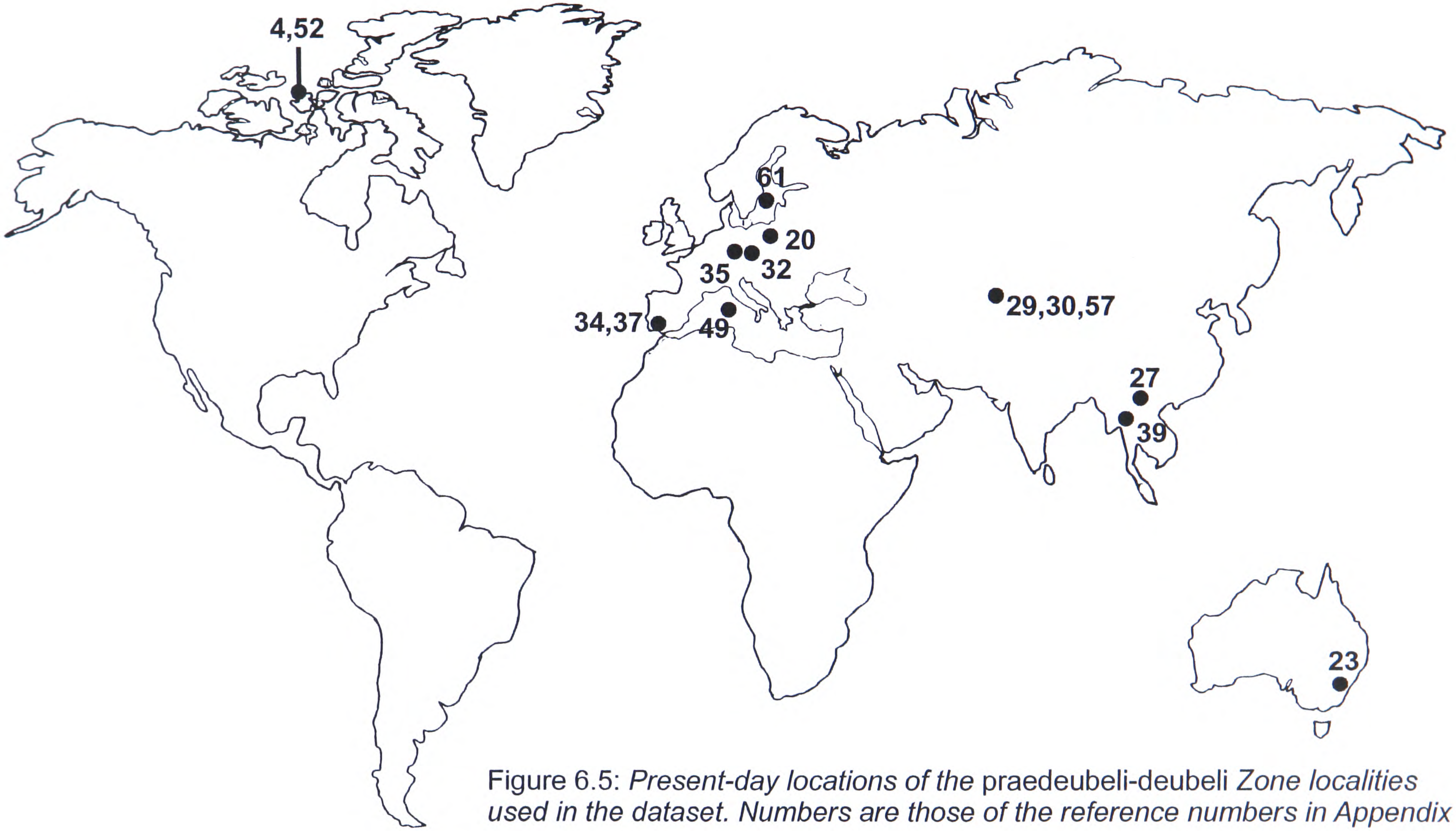


Figure 6.5: *Present-day locations of the* praedeubeli-deubeli *Zone localities used in the dataset. Numbers are those of the reference numbers in Appendix 1.*

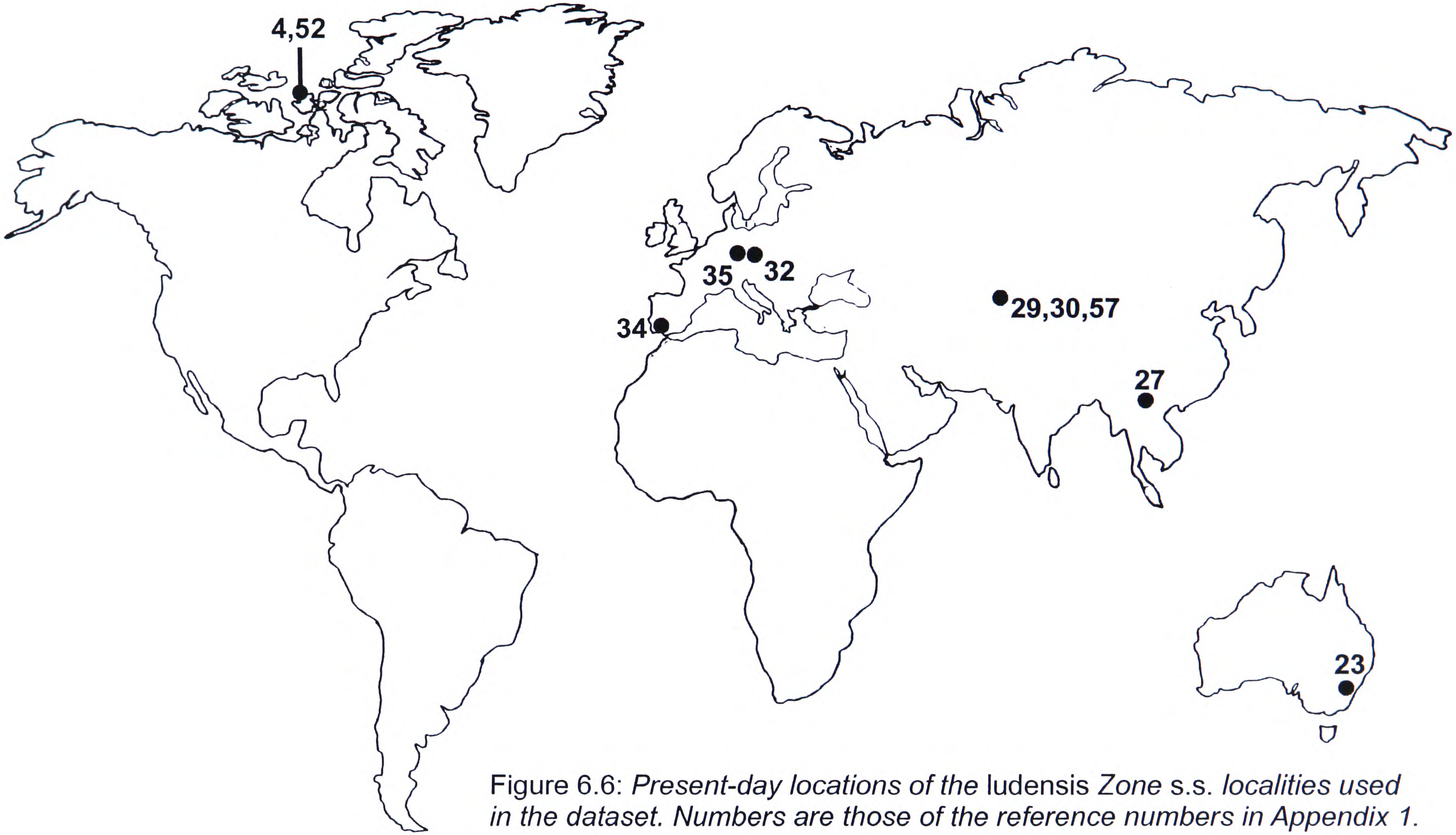


Figure 6.6: *Present-day locations of the* ludensis *Zone* s.s. *localities used in the dataset. Numbers are those of the reference numbers in Appendix 1.*

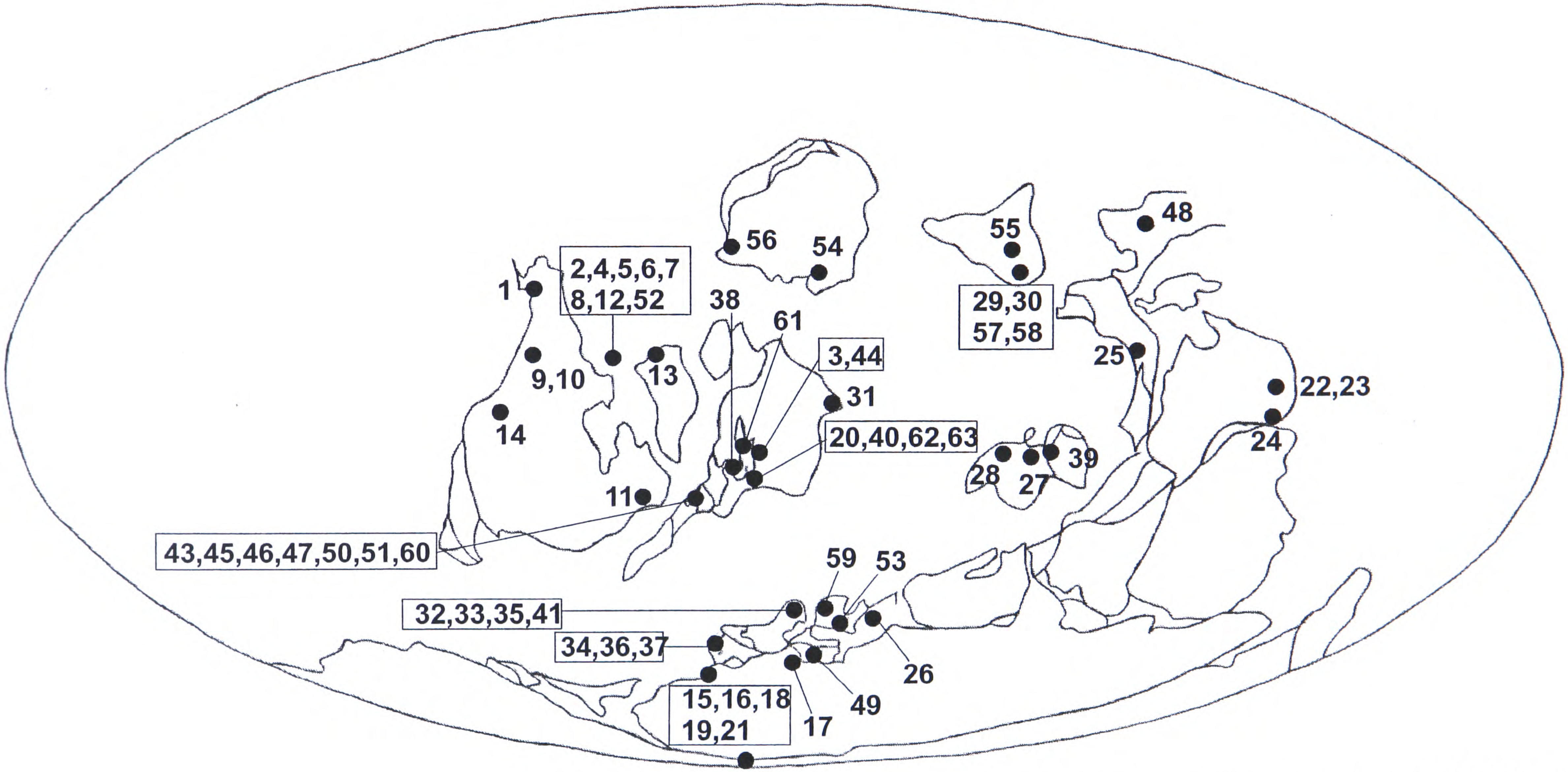


Figure 6.7: *Silurian locations of all the localities used in the dataset. Numbers are those of the reference numbers in Appendix 1. Map redrawn from the Paleomap website (www.scotese.com).*

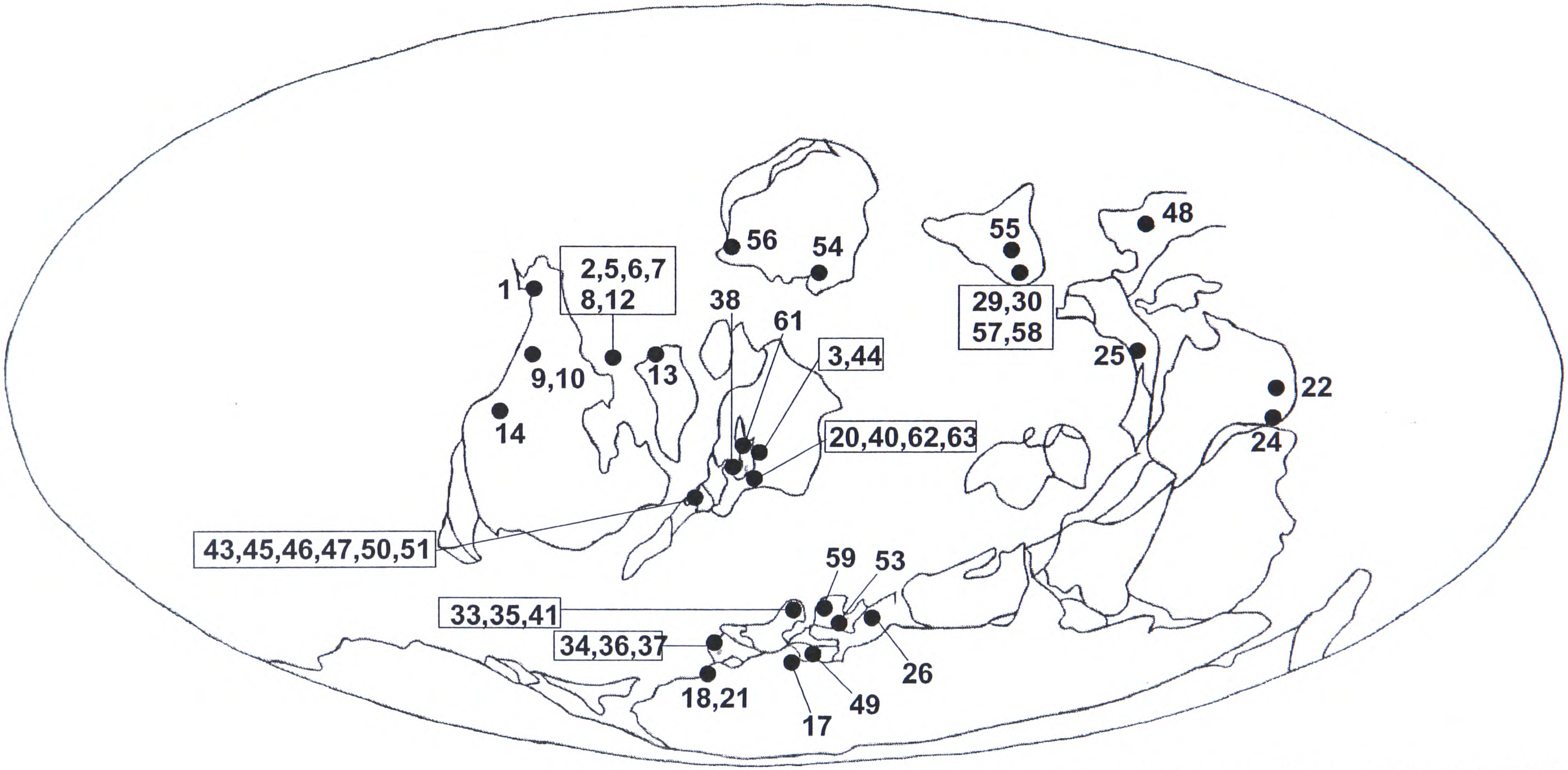


Figure 6.8: *Silurian locations of the* lundgreni *Zone localities used in the dataset. Numbers are those of the references in Appendix 1. Map redrawn from the Paleomap website (www.scotese.com).*

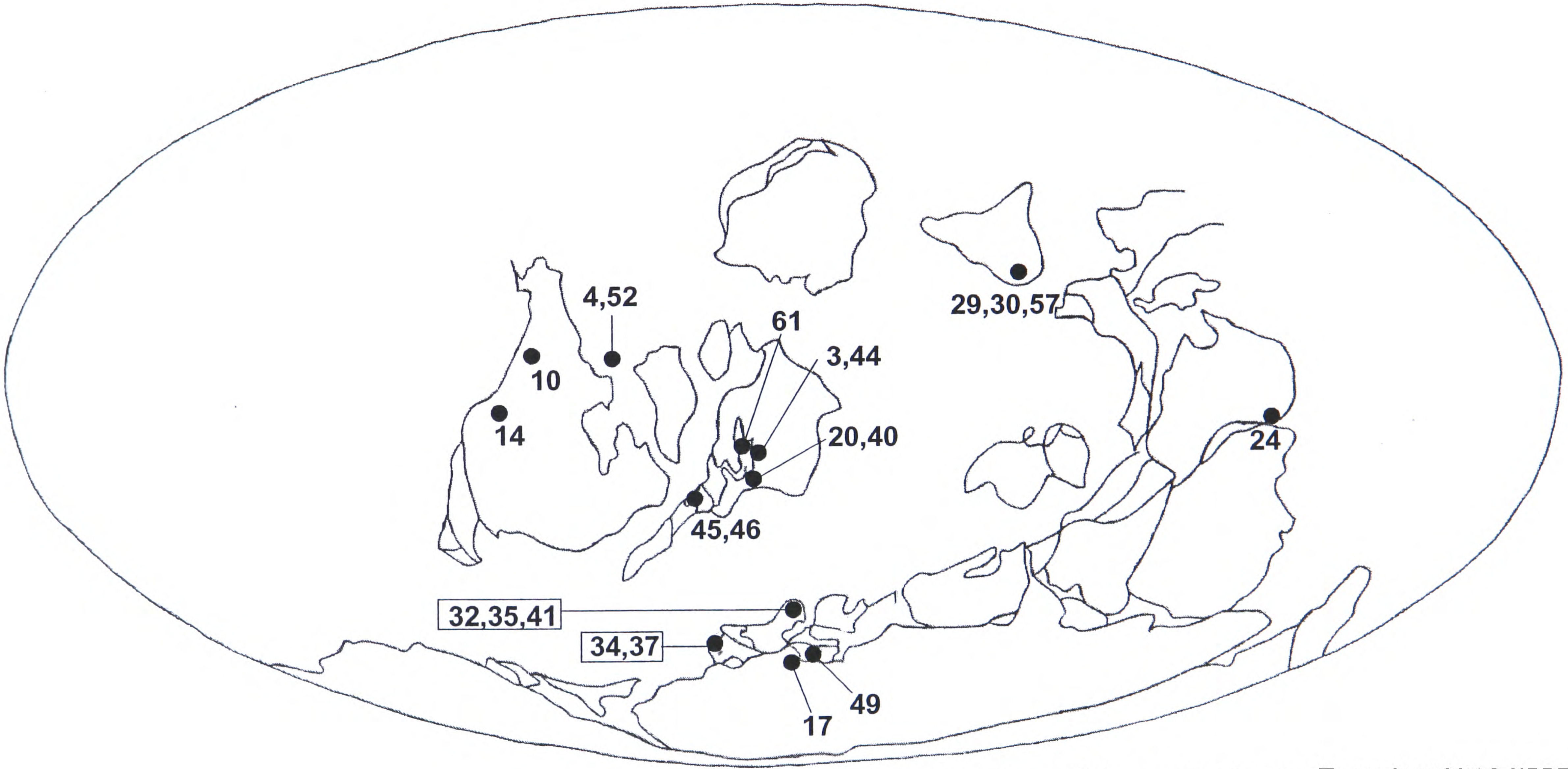


Figure 6.9: *Silurian locations of the* parvus-nassa *Zone localities used n the dataset. Numbers are those of the references in Appendix 1. Map redrawn from the Paleomap website (www.scotese.com).*

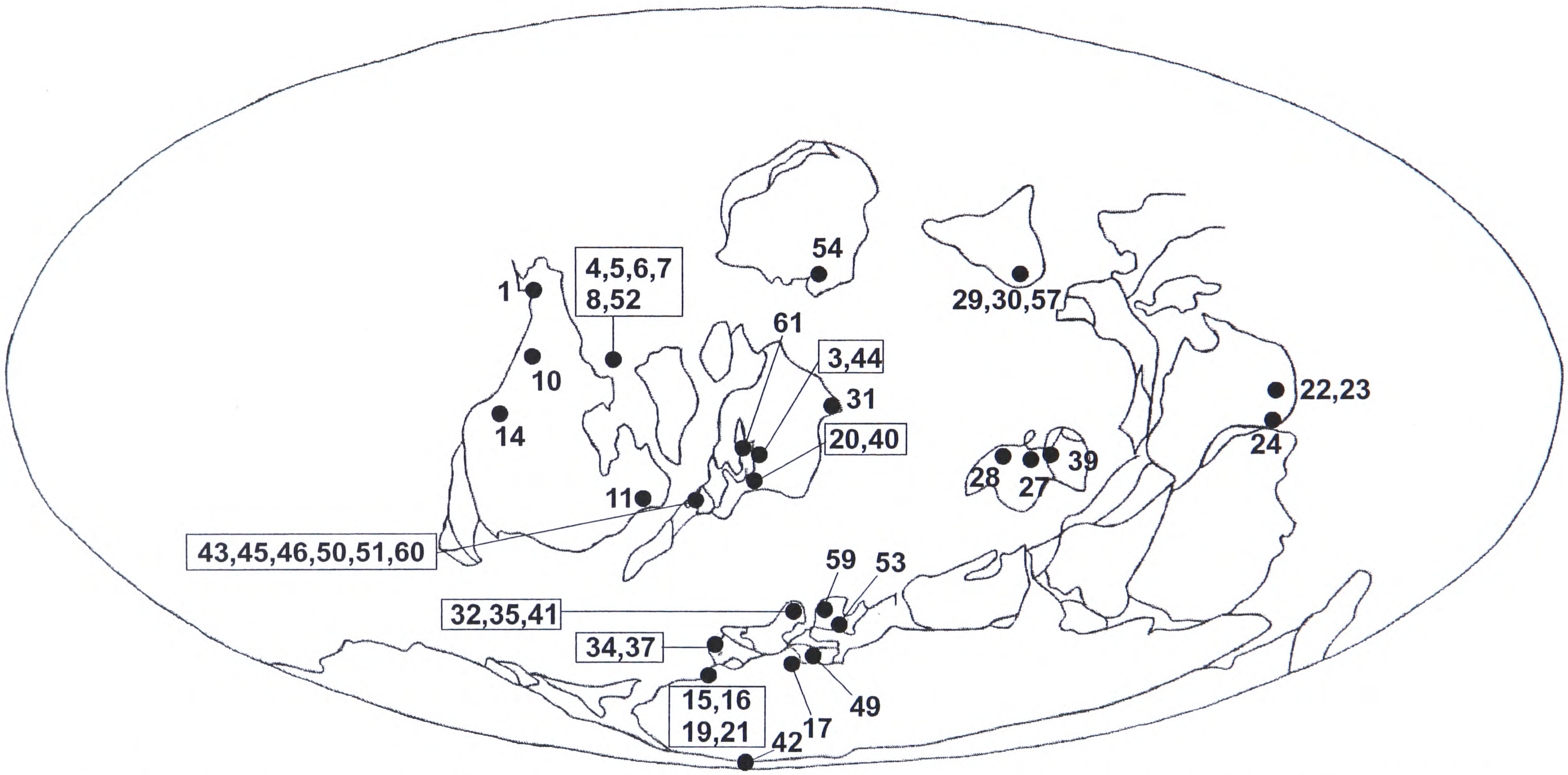


Figure 6.10: *Silurian locations of the* ludensis *Zone* s.l. *localities used in the dataset. Numbers are those of the references in Appendix 1. Map redrawn from the Paleomap website (www.scotese.com).*

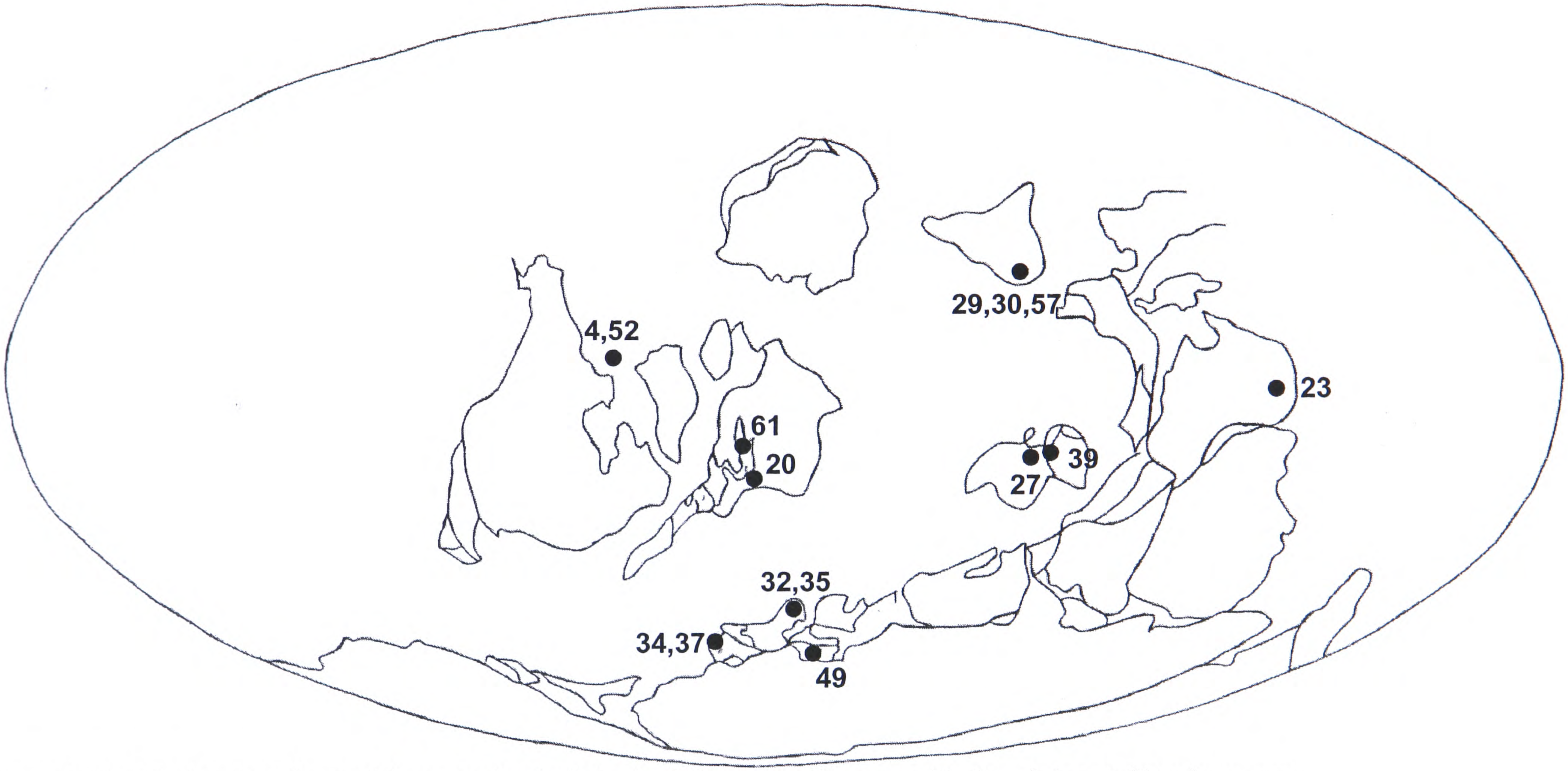


Figure 6.11: *Silurian locations of the praedeubeli-deubeli Zone localities used in the dataset. Numbers are those of the references in Appendix 1. Map redrawn from the Paleomap website (www.scotese.com).*

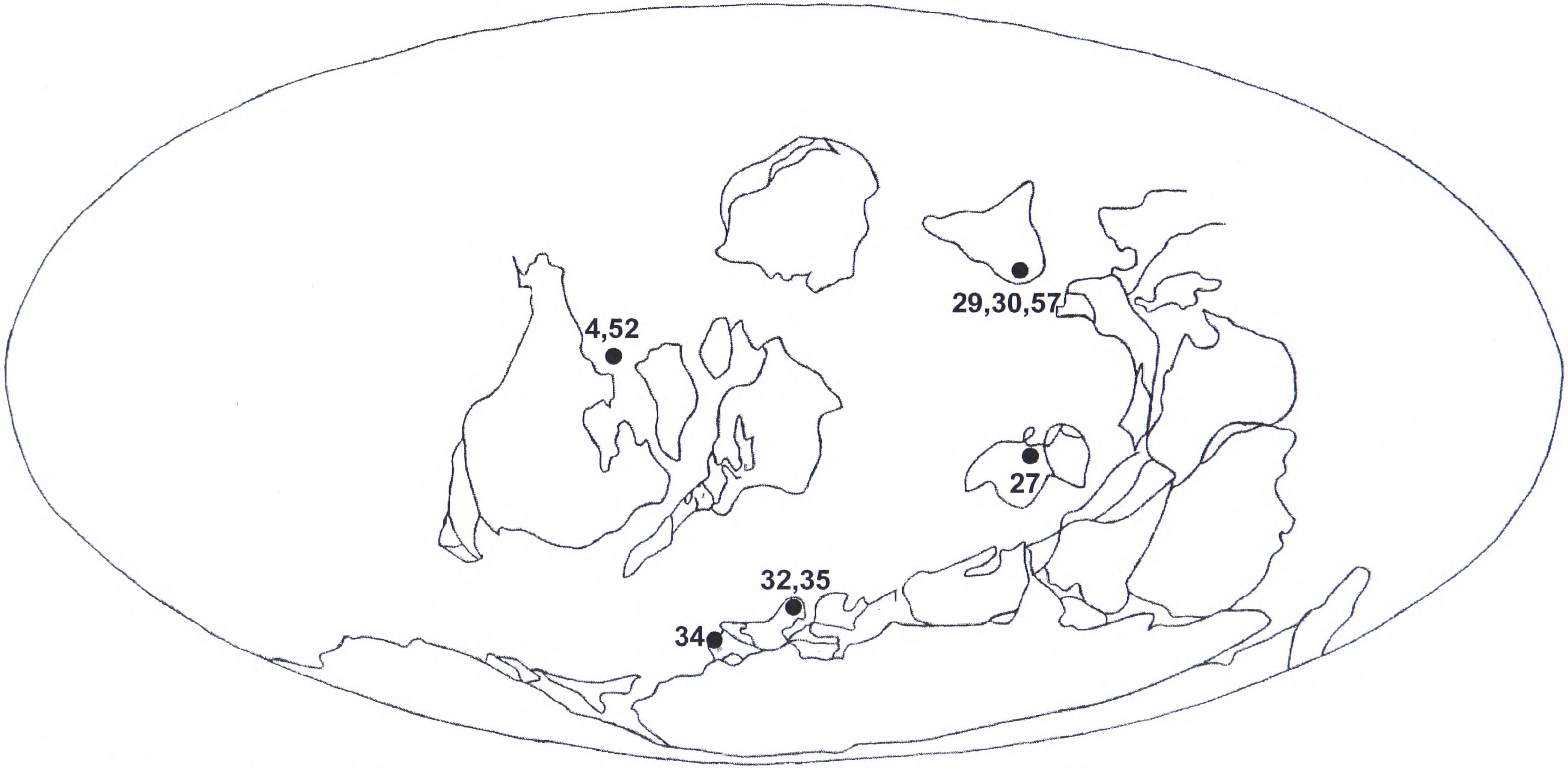


Figure 6.12: *Silurian locations of the* ludensis *Zone* s.s. *localities used in the dataset. Numbers are those of the references in Appendix 1. Map redrawn from the Paleomap website (www.scotese.com).*

In the *parvus-nassa* Zone diversity is surprisingly high, with fourteen monograptid and twelve retiolitid species at twenty-two localities. Eighteen of these species occur at only one locality. The exceptions are *Pristiograptus parvus* (nine localities), *P. dubius* (eighteen localities), *P. jaegeri* (five localities), *P. lodenicensis* (two localities), *P. pseudodubius* (four localities), *Monograptus flemingii* (two localities), *Pseudoplectograptus praemacilentus* (three localities) and *Gothograptus nassa* (twenty localities). The highest diversity at any one locality is ten species at Locality 3 (Lithuania). From this it appears that *P. parvus* is not a particularly useful marker of the *parvus-nassa* Zone, being present at less than half of the localities. The actual diversity of pristiograptids given here may be an overestimate, as some species may be synonyms of others, e.g. *P. parvus* and *P. pseudodubius*. However, most of the references used in the dataset did not give taxonomic descriptions, so it was impossible to synonymise.

In the *ludensis* Zone *s.l.* diversity is fifty-eight species at forty-six localities. The highest diversity at any one locality is twenty species at Locality 52 (Arctic Canada).

Table 6.1: *Number of species per zone for all graptoloid subfamilies. Neo.= Neodiplograptidae, Ret. = Retiolitinae, Plect. = Plectograptinae, Cyrt. = Cyrtograptinae, Mon. = Monograptinae.*

	Number of species					
Zone	**Neo.**	**Ret.**	**Plect.**	**Cyrt.**	**Mon.**	**Total**
lundgreni	1	5	20	14	36	**76**
parvus-nassa	0	0	12	0	14	**26**
ludensis s.l.	1	0	25	1	30	**57**
praedeubeli-deubeli	0	0	19	0	14	**33**
ludensis s.s.	0	0	12	0	9	**21**
Total	**1**	**5**	**41**	**14**	**57**	**117**

Figures 6.13 to 6.15 and tables 6.2 to 6.4 show the numbers of species surviving between zones, not including Lazarus taxa. The Retiolitinae are not shown, as none of them survive the end of the *lundgreni* Zone. The Neodiplograptidae are also not shown, because this family is only represented by one species at this time. Survivorship appears higher for the *lundgreni* Zone to the *ludensis* Zone *s.l.* than for the *lundgreni* Zone to the *parvus-nassa* Zone because the *parvus-nassa* Zone was not recognised in many places. Retiolitids and monograptids show a fall in diversity

during the *parvus-nassa* Zone, but swiftly rebound, with diversity in the *ludensis* Zone *s.l.* being almost equal to that in the *lundgreni* Zone. From these data it is not possible to say how quickly diversity recovers – data on changes in the number of species with time within the *ludensis* Zone *s.l.* would be required for that. It is possible to obtain some estimate using data from the *praedeubeli-deubeli* and *ludensis s.s.* zones, the subdivisions of the *ludensis* Zone *s.l.* The *praedeubeli-deubeli* Zone contains thirty-three species at fourteen localities and the *ludensis* Zone *s.s.* twenty-one at nine localities. Thus it appears that diversity had recovered early in the *ludensis* Zone *s.l.* and fell again later in the zone. Actual diversity during the *praedeubeli-deubeli* Zone was almost certainly greater than thirty-three species, the small number reflecting the small number of localities sampled. The apparent diversity fall between the *praedeubeli-deubeli* and *ludensis s.l.* zones may be a real pattern, or it may be an artefact resulting from the small number of *ludensis* Zone *s.s.* localities in the sample. More data are needed to solve these problems; this will only come from biostratigraphic studies in regions where the *ludensis* Zone *s.l.* is not subdivided at present.

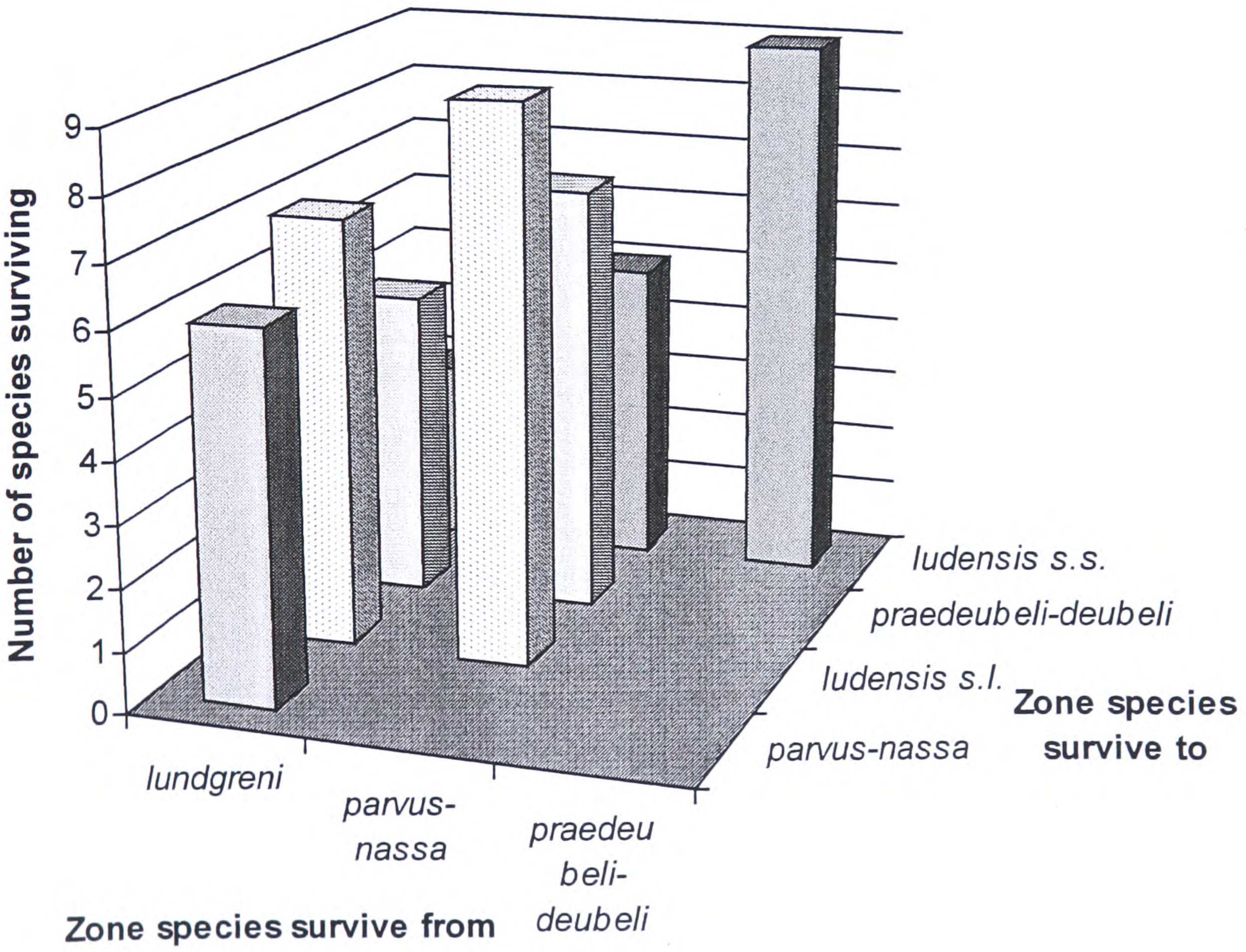


Figure 6.13: *Number of species surviving zone to zone for the Plectograptinae.*

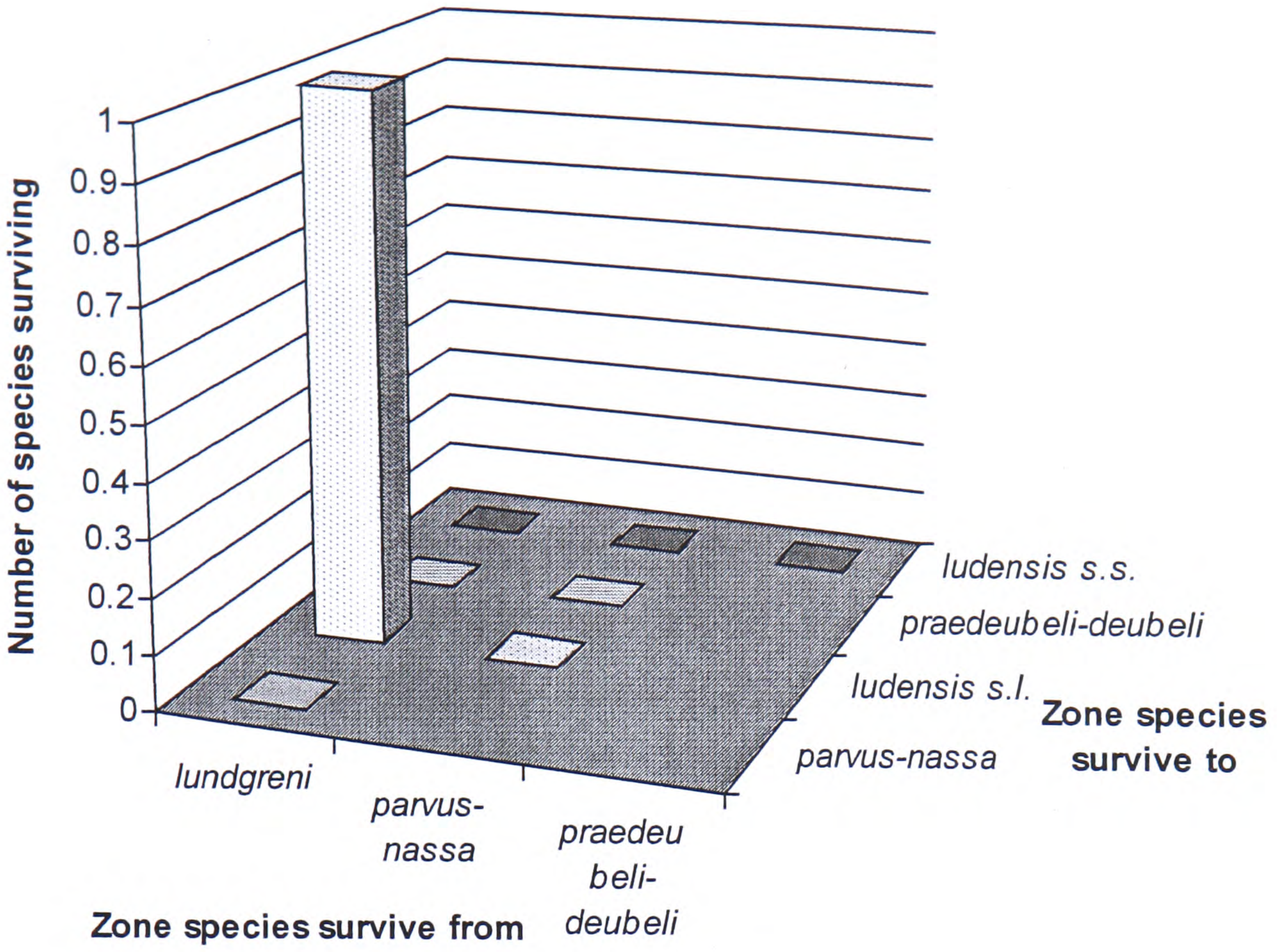


Figure 6.14: *Number of species surviving zone to zone for the Cyrtograptinae.*

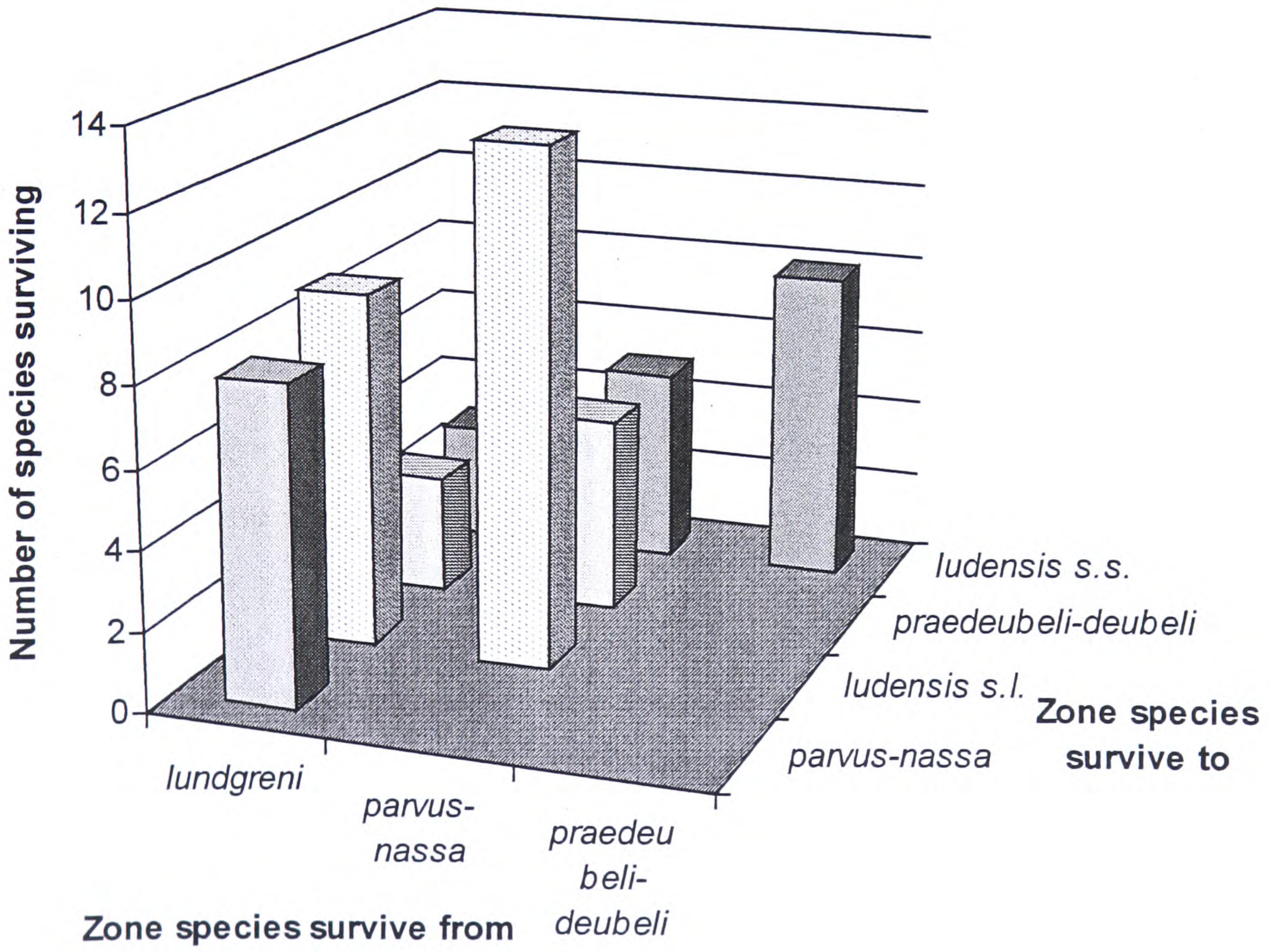


Figure 6.15: *Number of species surviving zone to zone for the Monograptinae.*

Table 6.2: *Number of species surviving zone to zone for the Plectograptinae.*

	Number of species surviving into zone			
Zone	***parvus-nassa***	***ludensis s.l.***	***praedeubeli-deubeli***	***ludensis s.s.***
lundgreni	6	7	5	3
parvus-nassa		9	7	5
praedeubeli-deubeli				9

Table 6.3: *Number of species surviving zone to zone for the Cyrtograptinae.*

	Number of species surviving into zone			
Zone	***parvus-nassa***	***ludensis s.l.***	***praedeubeli-deubeli***	***ludensis s.s.***
lundgreni	0	1	0	0
parvus-nassa		0	0	0
praedeubeli-deubeli				0

Table 6.4: *Number of species surviving zone to zone for the Monograptinae.*

	Number of species surviving into zone			
Zone	***parvus-nassa***	***ludensis s.l.***	***praedeubeli-deubeli***	***ludensis s.s.***
lundgreni	8	9	3	3
parvus-nassa		13	5	5
praedeubeli-deubeli				8

The percentage survivorship from the *lundgreni* Zone to the *parvus-nassa* and *ludensis s.l.* zones is equal for retiolitids and monograptids, but much lower for cyrtograptids (Tables 6.5 to 6.7). For the monograptids and retiolitids, the survivorship from the *parvus-nassa* Zone to the *ludensis* Zone *s.l.* is high, indicating either that whatever factor(s) caused the *lundgreni* event had ceased, or that the majority of species were resistant to them.

Table 6.5: *Percentage survivorship zone to zone for the Plectograptinae.*

	Percentage of species surviving into zone			
Zone	***parvus-nassa***	***ludensis s.l.***	***praedeubeli***	***ludensis s.s.***
lundgreni	23	27	19	12
parvus-nassa		75	58	42
praedeubeli-deubeli				47

Table 6.6: *Percentage survivorship zone to zone for the Cyrtograptinae.*

	Percentage of species surviving into zone			
Zone	***parvus-nassa***	***ludensis s.l.***	***praedeubeli***	***ludensis s.s.***
lundgreni	0	7	0	0
parvus-nassa		0	0	0
praedeubeli-deubeli				0

Table 6.7: *Percentage survivorship zone to zone for the Monograptinae.*

	Percentage of species surviving into zone			
Zone	***parvus-nassa***	***ludensis s.l.***	***praedeubeli***	***ludensis s.s.***
lundgreni	22	25	8	8
parvus-nassa		93	36	36
praedeubeli-deubeli				57

The species that survived from the *lundgreni* Zone to the *parvus-nassa* or *ludensis s.l.* zones are as follows. In the monograptids, *Colonograptus deubeli, Monograptus flemingii, M. priodon, Pristiograptus dubius, P. jaegeri, P. lodenicensis, P. parvus, P. praedubius, P. pseudodubius* and *Testograptus testis*. In the retiolitids, *Cometograptus marsupium, Com. nevadensis, Gothograptus nassa, G. pseudospinosus, Pseudoplectograptus praemacilentus, Sokolovograptus lejskoviensis* and *Spinograptus clathrospinosus*. The neodiplograptid *Neoglyptograptus sussmilchi* also survived. The only cyrtograptid survivor is *Cyrtograptus ellesae*. Some of the records of these species either before or after the lundgreni event are of the "ex gr." or "aff." type, for example the record of *Colonograptus deubeli* during the *lundgreni* Zone is of *Colonograptus* aff. *deubeli* from North Wales (Warren 1971, reference 45), and the cyrtograptid survivor is *Cyrtograptus* ex gr. cf. *ellesae* from New South Wales (Rickards *et al*. 1995a, reference 22).

These results illustrate the importance of looking at species diversity globally when studying extinction events. Someone looking at an individual section would not see the full diversity present globally. The results also illustrate the usefulness of isolated faunas – the highest diversities at single localities in the *lundgreni* and *ludensis s.l.* zones are in Arctic Canada, where isolatable graptoloids occur. Some species, especially many retiolitids, are known only from isolated faunas.

There are few Lazarus taxa (meaning, in this context, species present in the *lundgreni* and *ludensis s.l.* zones but not in the *parvus-nassa* Zone). The species in question are *Neoglyptograptus sussmilchi, Cometograptus marsupium, Sokolovograptus textor, Cyrtograptus ellesae, Monograptus priodon* and *Testograptus testis*. With the exception of *M. priodon*, these examples are all from Australia, and their absence from the *parvus-nassa* Zone is probably because that zone has not yet been recognised in Australia.

6.1.1 Endemism

Graptoloids are frequently said to be a cosmopolitan group. This is clearly the case for some species, but not all. (See section 2.5 for background on graptoloid biogeography.) As being endemic is frequently cited as a risk factor for extinction, it was decided to look at the amount of endemism present during and after the *lundgreni* Zone. The Silurian world was divided into three areas, Laurentia-Baltica, North Africa-Southern Europe, and Kazakhstan-North China-Australia (Figure 6.16) and the number of areas each species occurred in was recorded (data in Appendix 4). The areas were divided on the basis of where deep oceans occur. Kazakhstan is included with Australia because of faunal similarities. The results are given in Table 6.8 and Figure 6.17.

These results show that endemism is high (at least 50%) for all subfamilies in all zones, except for the Cyrtograptinae in the *lundgreni* Zone. For the Plectograptinae, percentage endemism is approximately the same in the *lundgreni* and *ludensis s.l.* zones, with a peak in the *nassa* Zone. For the Monograptinae, percentage endemism

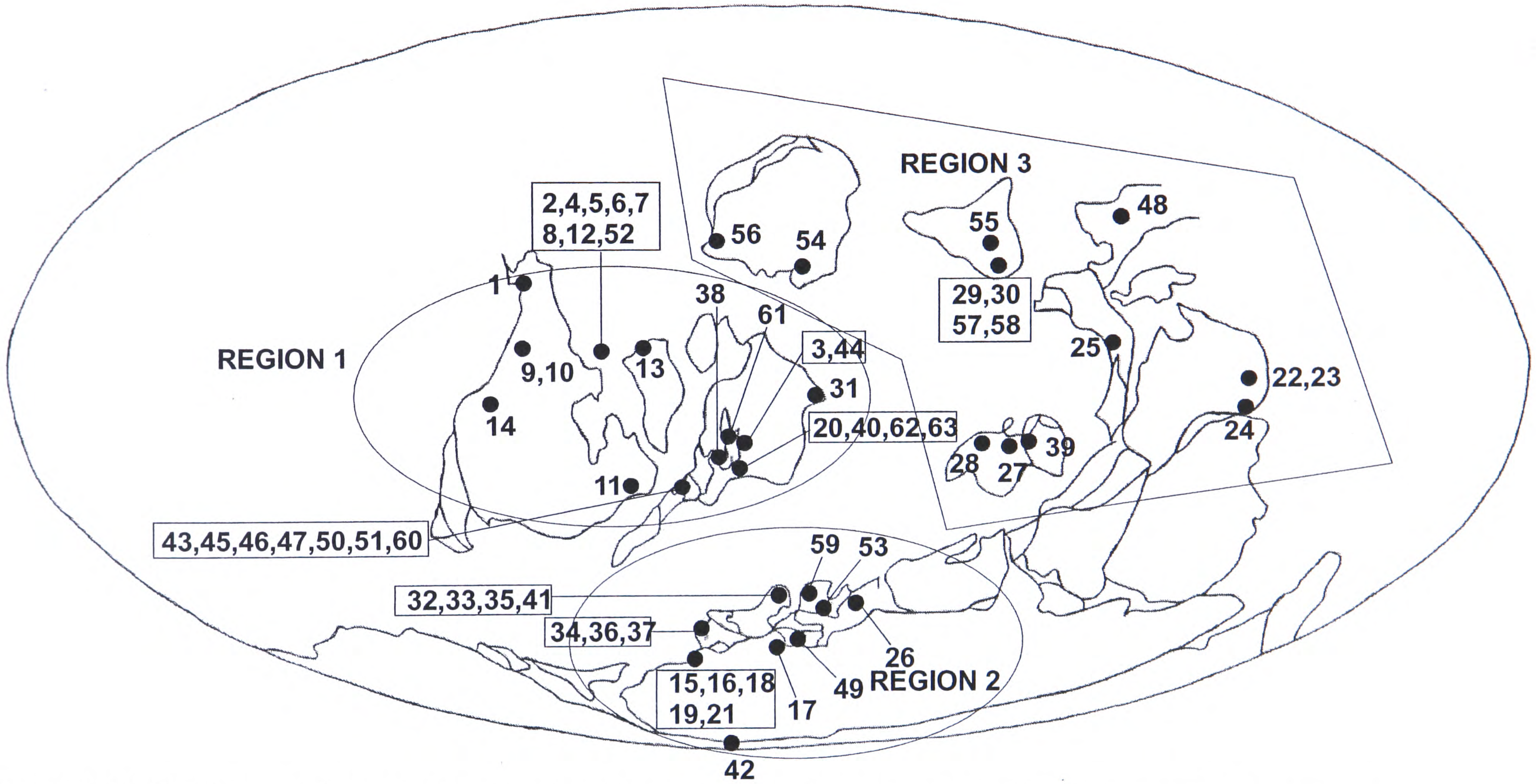


Figure 6.16: *The three regions used in the geographic study. Numbers are those of the references in Appendix 1. Map redrawn from the Paleomap website (www.scotese.com).*

is approximately constant through all three zones. This means that there was an equal percentage of cosmopolitan monograptid species in all three zones, but there were fewer cosmopolitan retiolitid species during the *parvus-nassa* Zone. This indicates that most retiolitid species had restricted distributions after the *lundgreni* extinction.

For retiolitids there is a taphonomic bias in that they are more easily found in isolated faunas rather than flattened ones. Isolatable graptoloids of this age only occur in Poland, Arctic Canada and Sweden, all part of the same area in this analysis. The presence of these faunas will increase the apparent endemism, because some species may only be found in isolated form. As isolatable faunas are only found in one area, these species will only be found in that one area, whereas they may occur in the other areas but not be found. In order to counteract this bias, the number of species in each area excluding faunas from Poland and Arctic Canada was counted. The results are given in Table 6.9 and graphically in Figure 6.18, and the differences between endemism with and without the isolated faunas are given in Table 6.10.

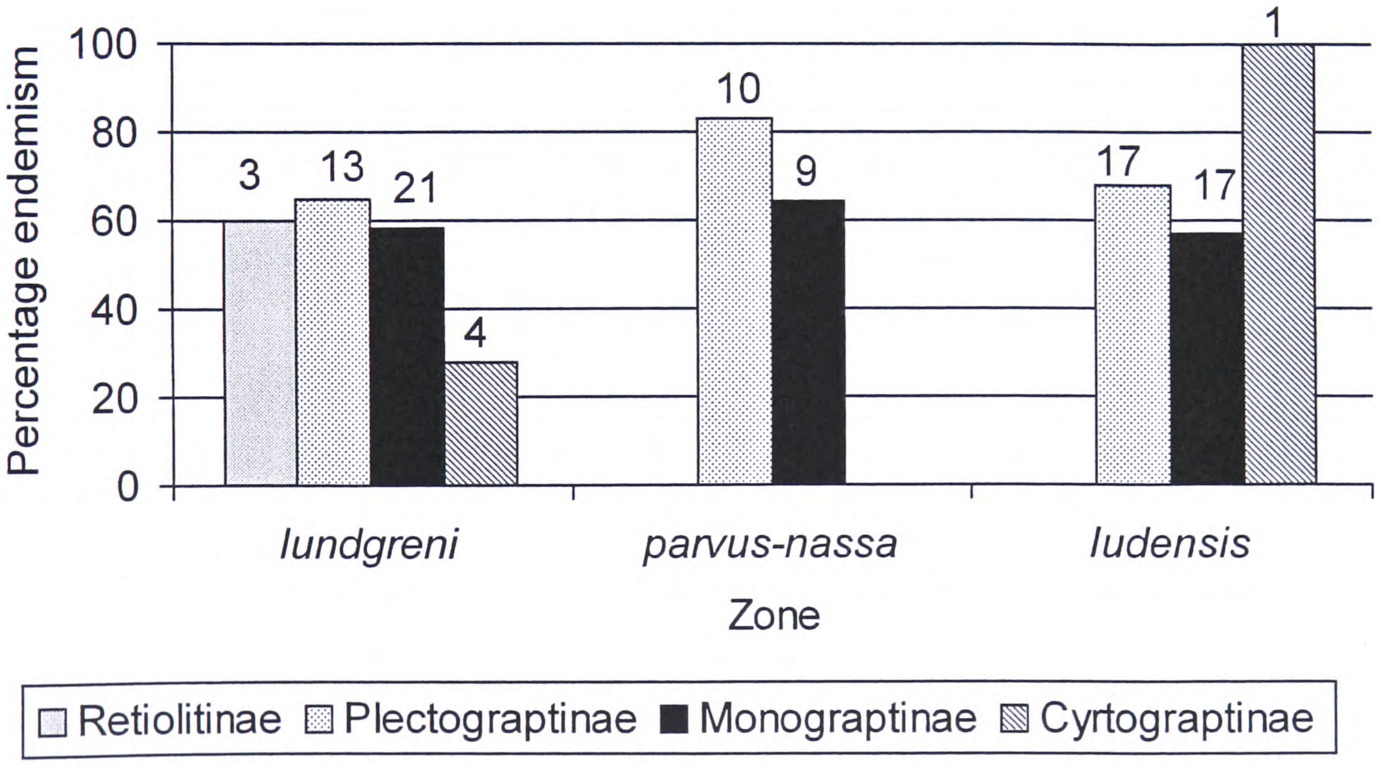


Figure 6.17: *Percentage endemism for the Retiolitidae, Monograptinae and Cyrtograptinae in the* lundgreni, parvus-nassa *and* ludensis s.l. *zones, including faunas with isolated graptoloids. Numbers are the numbers of endemic species.*

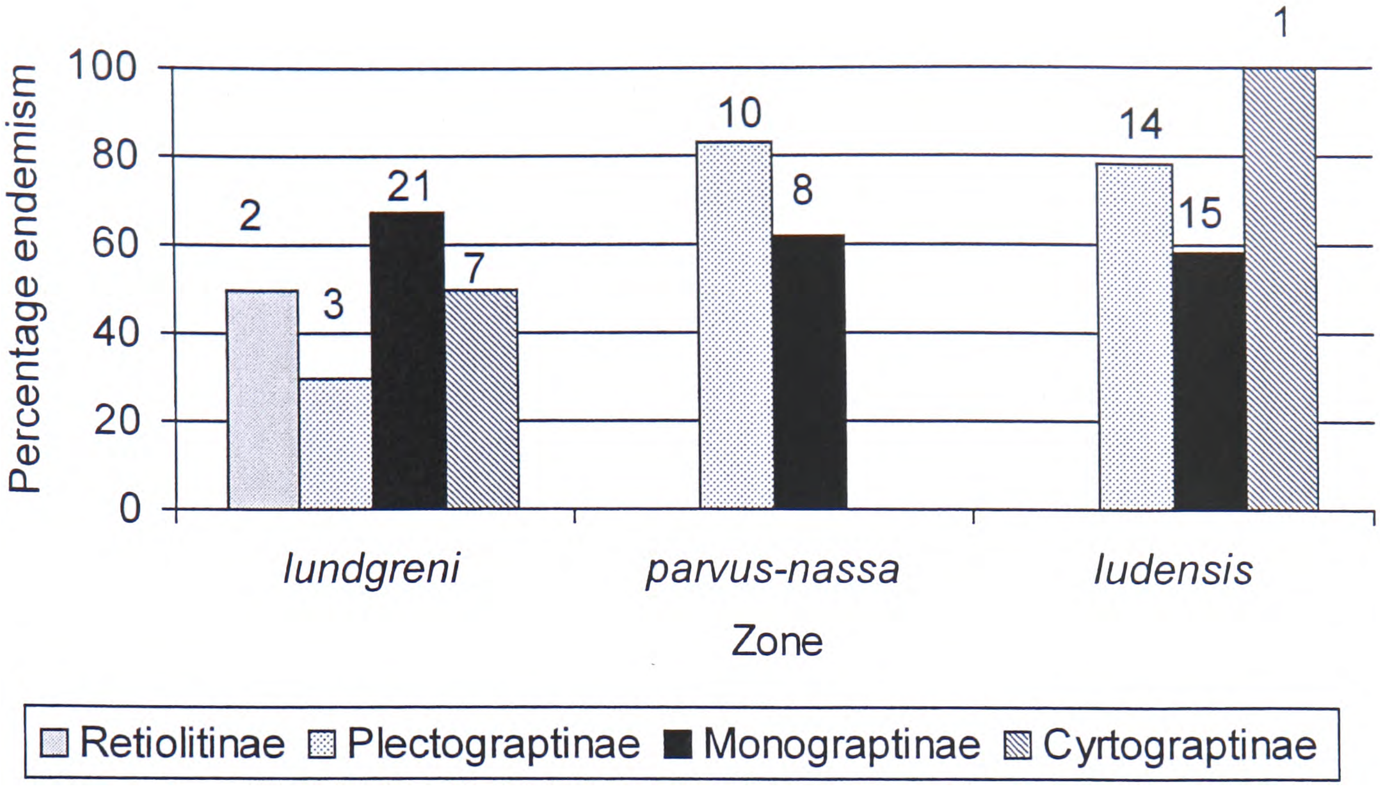


Figure 6.18: *Percentage endemism for the Retiolitidae, Monograptinae and Cyrtograptinae in the* lundgreni, parvus-nassa *and* ludensis s.l. *zones, excluding faunas with isolated graptoloids.*

Table 6.8: *Number of species found in one, two and three areas for all subfamilies in the* lundgreni *to* ludensis *s.l. zones, including faunas with isolated graptoloids. A species is classed as endemic if it occurs in only one area.*

		Number of species found in				
Zone	**Subfamily**	**1 area**	**2 areas**	**3 areas**	**Total**	**% endemism**
lundgreni	Retiolitinae	3	1	1	5	60
	Plectograptinae	13	4	3	20	65
	Monograptinae	21	10	5	36	58
	Cyrtograptinae	4	6	4	14	28
parvus-nassa	Plectograptinae	10	1	1	12	83
	Monograptinae	9	4	1	14	64
ludensis s.l.	Plectograptinae	17	4	4	25	68
	Monograptinae	17	7	6	30	57
	Cyrtograptinae	1	0	0	1	100
praedeubeli-deubeli	Plectograptinae	13	5	1	19	68
	Monograptinae	7	3	4	14	50
ludensis s.s.	Plectograptinae	9	3	0	12	75
	Monograptinae	4	1	4	9	44

Table 6.9: *Number of species found in one, two and three areas for all subfamilies in the* lundgreni *to* ludensis *s.l. zones, excluding faunas with isolated graptoloids. A species is classed as endemic if it occurs in only one area.*

		Number of species found in				
Zone	**Subfamily**	**1 area**	**2 areas**	**3 areas**	**Total**	**% endemism**
lundgreni	Retiolitinae	2	2	0	4	50
	Plectograptinae	3	5	2	10	30
	Monograptinae	21	5	5	31	67
	Cyrtograptinae	7	3	4	14	50
parvus-nassa	Plectograptinae	10	1	1	12	83
	Monograptinae	8	4	1	13	62
ludensis s.l.	Plectograptinae	14	3	1	18	78
	Monograptinae	15	5	6	26	58
	Cyrtograptinae	1	0	0	1	100
praedeubeli-deubeli	Plectograptinae	9	0	1	10	90
	Monograptinae	7	2	2	11	64
ludensis s.s.	Plectograptinae	7	1	0	8	88
	Monograptinae	1	5	0	6	16

Table 6.10: *The difference in the number of species between faunas with and faunas without isolated graptoloids (Table 6.08 minus Table 6.09). Negative numbers represent a decrease in the number of species found in 1, 2 or 3 areas; positive numbers represent an increase. A species is classed as endemic if it occurs in only one area.*

	Number of species found in					
Zone	**Subfamily**	**1 area**	**2 areas**	**3 areas**	**Total**	**% endemism**
lundgreni	Retiolitinae	-1	+1	-1	-1	-10
	Plectograptinae	-10	+1	-1	-10	-35
	Monograptinae	0	-5	0	-5	+9
	Cyrtograptinae	+3	-3	0	0	+22
parvus-nassa	Plectograptinae	0	0	0	0	0
	Monograptinae	-1	0	0	-1	-2
ludensis s.l.	Plectograptinae	-3	-1	-3	-7	+10
	Monograptinae	-2	-2	0	-4	+1
	Cyrtograptinae	0	0	0	0	0
praedeubeli-deubeli	Plectograptinae	-4	-5	0	-9	+22
	Monograptinae	0	-1	-2	-3	+14
ludensis s.s.	Plectograptinae	-2	-2	0	-4	+13
	Monograptinae	-3	+4	-4	-3	+28

A comparison of the percentage endemism with and without isolated faunas reveals that, for the retiolitids, apparent endemism is decreased during the *lundgreni* Zone, whereas for monograptids and cyrtograptids it is increased. Many retiolitid species are only known from isolated faunas. It is possible that these species did occur globally but have not been found. If this is the case, endemism will have been overestimated.

6.2 Hypotheses to be tested

The hypotheses that will be tested are:

1. Extinction is random, i.e. all species have an equal probability of extinction.
2. There is a correlation between geographical distribution and extinction probability.
3. Rare species are more likely to go extinct than common species.
4. There are latitudinal variations in extinction patterns.
5. K-selected species are more likely to go extinct than r-selected ones.

These hypotheses are discussed in more detail below.

6.2.1 Is extinction random?

Random extinction means that every species has an equal probability of going extinct. That extinction is random is the null hypothesis when considering the causes of extinctions. If extinction is not random, this implies that there is something about some taxa that makes them more likely to go extinct than other taxa.

It is appropriate to test for randomness of extinction at the genus, subfamily and family levels, because extinction may be random at some taxonomic levels, but not at others. For example, a family may consist of two genera, one susceptible to extinction and the other resistant. When combined, the extinction rates for the genera may give an average extinction rate for the family. See Table 6.11 for a hypothetical example.

Table 6.11: *With an average per-genus and per-family extinction rate of 50% of species, in this example the extinction rates differ significantly at generic level, but not at family level.*

	Number of species		
	Genus 1	**Genus 2**	**Total**
Extinct	18	2	20
Survive	2	18	20
Total	20	20	40

Tables of results and of statistical analyses on extinction rates at the family, subfamily and genus level are given in Tables 6.12 to 6.18. The null hypothesis for every table is that extinction is random. This was confirmed statistically at the family and subfamily level. At the genus level within the Monograptidae and Retiolitidae the expected numbers are too small for statistical analysis. However, within the Monograptidae most genera have the majority of species becoming extinct, the exception being *Pristiograptus*, in which the majority of species (six out of nine) survive. Thus it appears that *Pristiograptus* is more resistant to extinction than the other genera. However, if *Pristiograptus* is oversplit taxonomically (and therefore there are fewer than nine species present in reality), the real survivorship rate may be somewhat lower.

Table 6.12: *Chi-squared analysis of extinction rate between families in* lundgreni *Zone graptoloids. Chi-squared = 0.33, with one degree of freedom. Probability is greater than 0.05, therefore the null hypothesis is not rejected.*

		Number of species		
		Monograptidae	**Retiolitidae**	**Total**
Extinct	**Obs.**	39	18	57
	Exp.	38	19	
Survive	**Obs.**	11	7	18
	Exp.	12	6	
Total		50	25	75

Table 6.13: *Chi-squared analysis of extinction rates between subfamilies in* lundgreni *Zone Retiolitidae. The exact method for 2x2 tables was used. Probability = 0.16, so the null hypothesis is not rejected.*

	Number of species		
	Retiolitinae	**Plectograptinae**	**Total**
Extinct	5	13	18
Survive	0	7	7
Total	5	20	25

Table 6.14: *Chi-squared analysis of extinction rates between subfamilies within the Monograptidae in the* lundgreni *Zone. In this case the chi-squared test could not be used as one of the expected numbers is less than five. The exact method for 2x2 tables was used instead. The probability of this table occurring is greater than 0.05, so the null hypothesis was not rejected.*

		Number of species		
		Monograptinae	**Cyrtograptinae**	**Total**
Extinct	**Obs.**	26	13	39
	Exp.	28.08	10.92	
Survive	**Obs.**	10	1	11
	Exp.	7.92	3.08	
Total		36	14	50

Table 6.15: *Extinction rates for genera in* lundgreni *Zone Monograptidae.* Pristio. = Pristiograptus, Cyrto. = Cyrtograptus.

		Number of species				
		***Monograptus* s.s.**	***Pristio.***	***Monoclimacis***	***Cyrto.***	**Total**
Extinct	**Obs.**	14	3	6	13	36
	Exp.	12.8	7.2	4.8	11.2	
Survive	**Obs.**	2	6	0	1	9
	Exp.	3.2	1.8	1.2	2.8	
Total		16	9	6	14	45

Table 6.16: *Generic assignments for* lundgreni *Zone monograptids.* Co. = Colonograptus, E. = Euroclimacis, M. = Monograptus, Mcl. = Monoclimacis, Med. = Mediograptus, P. = Pristiograptus, T. = Testograptus. *Species in bold survive the* lundgreni *event.*

***Monograptus* s.s.**	***Pristiograptus***	***Monoclimacis***	**Not assigned to a genus**
M. ambiguus	***P. dubius***	*E. adunca*	***Co. deubeli***
M. bogdanovi	***P. jaegeri***	*Mcl. flumendosae*	*M? antennularius*
M. boreus	***P. lodenicensis***	*Mcl. hemipristis*	*M? biglossa*
M. firmus festinolatus	*P. meneghini*	*Mcl. oradovskayae*	*Med. retroflexus*
M. flemingii	***P. parvus***	*Mcl. simplex*	***T. testis***
M. instrenuus	***P. praedubius***	*Mcl. vomerinus*	
M. irfonensis	***P. pseudodubius***		
M. munchi	*P. sarduous*		
M. mutuliferus longissimus	*P. sumptuosus*		
M. nganasanicus			
M. opimus			
M. priodon			
M. proboscidatus			
M. riccartonensis			
M. shakhmardanicus			
M. subflexilis			

Table 6.17: *Extinction rates for genera in* lundgreni *Zone Retiolitinae.*

	Number of species			
	Eisenackograptus	***Paraplectograptus***	***Retiolites***	**Total**
Extinct	1	3	1	5
Survive	0	0	0	0
Total	1	3	1	5

Table 6.18: *Extinction rates for genera in* lundgreni *Zone Plectograptinae.* Com. = Cometograptus, G. = Gothograptus, Pl. = Plectograptus, Ps. = Pseudoplectograptus, Sa. = Sagenograptus, So. = Sokolovograptus, Sp. = Spinograptus.

	Number of species							
	Com.	**G.**	***Pl.***	***Ps.***	***Sa.***	***So.***	***Sp.***	**Total**
Extinct	4	3	2	2	1	1	0	13
Survive	2	2	0	1	0	1	1	8
Total	6	5	2	3	1	2	1	21

6.2.2 Does geographical distribution affect extinction?

Genera containing species that all have a narrow geographic range may be more extinction-prone than those that have widely distributed species (McKinney 1995). Theoretically, a taxon with a wide geographical range is more likely to survive an extinction event than a taxon with a narrow range, because in the wide range there is a greater chance of a refugium existing (Rosenzweig 1995 p.120) This has been shown to be true for some taxa in some extinctions, for example bivalves at the Cretaceous-Tertiary boundary (Jablonski & Raup 1995). In view of this, graptoloids with a wide distribution would be expected to survive the *lundgreni* event and those with a narrow distribution to become extinct.

In order to test this hypothesis the same three areas were used as in Section 6.1.1. Any species found in more than one of these areas was classed as widely distributed. The hypothesis was tested at the family level for the Monograptidae and Retiolitidae and at subfamily level for the Monograptidae. The numbers at genus level and at subfamily level for the Retiolitidae were too small for statistical analysis. The results are given in Tables 6.19 to 6.28. The analysis was performed both including and excluding data from isolated faunas, because some species, especially retiolitids, are known only from isolated faunas. As isolated faunas are geographically restricted, some species appear to be restricted geographically when they may have occurred more widely but have not been found in most areas. The null hypothesis in each case was that extinction is random with respect to geographical area.

For the retiolitids the null hypothesis is rejected when considering both isolated and non-isolated faunas (Tables 6.19 and 6.20). Thus it appears that having a narrow geographic range did increase extinction probability for the retiolitids.

Table 6.19: *Analysis of extinction patterns with respect to area for* lundgreni *Zone Retiolitidae, including faunas with isolated graptoloids. As expected numbers were too small to use chi-squared, the exact method for 2x2 tables was used. $p < 0.01$, therefore the null hypothesis is rejected.*

	Number of species		
	1 area	**>1 area**	**Total**
Extinct	15	3	18
Survive	1	6	7
Total	16	9	25

Table 6.20: *Analysis of extinction patterns with respect to area for* lundgreni *Zone Retiolitidae, excluding faunas with isolated graptoloids. As expected numbers were too small to use chi-squared, the exact method for 2x2 tables was used. $p = 0.03$, therefore the null hypothesis is rejected.*

	Number of species		
	1 area	**>1 area**	**Total**
Extinct	5	3	8
Survive	0	6	6
Total	5	9	14

For the cyrtograptids, as only one species survives, it is not possible to analyse the data statistically (Tables 6.21 and 6.22). However, as most cyrtograptids are widespread (ten of fourteen species), it appears that being widespread did not help them avoid extinction.

Table 6.21: *Data on extinction patterns with respect to area for* lundgreni *Zone Cyrtograptinae, including faunas with isolated graptoloids.*

		Number of species		
		1 area	**>1 area**	**Total**
Extinct	**Observed**	4	9	13
Survive	**Observed**	0	1	1
Total		4	10	14

Table 6.22: *Data on extinction patterns with respect to area for* lundgreni *Zone Cyrtograptinae, excluding faunas with isolated graptoloids.*

		Number of species		
		1 area	**>1 area**	**Total**
Extinct	**Observed**	7	6	13
Survive	**Observed**	0	1	1
Total		7	7	14

For the monograptids and cyrtograptids together, and for the Monograptinae alone, the data are not statistically significant (Tables 6.23 to 6.26). It therefore appears that geographical range did not affect extinction probabilities for the Monograptidae.

Table 6.23: *Analysis of extinction patterns with respect to area for* lundgreni *Zone Monograptidae, including faunas with isolated graptoloids. Chi-squared = 0.24, with one degree of freedom. p > 0.05, therefore the null hypothesis is not rejected.*

		Number of species		
		1 area	**>1 area**	**Total**
Extinct	**Observed**	21	18	39
	Expected	20.28	18.72	
Survive	**Observed**	5	6	11
	Expected	5.72	5.28	
Total		26	24	50

Table 6.24: *Analysis of extinction patterns with respect to area for* lundgreni *Zone Monograptidae, excluding faunas with isolated graptoloids. As expected numbers were too small to use chi-squared, the exact formula for 2x2 tables was used. p > 0.05, therefore the null hypothesis is not rejected.*

		Number of species		
		1 area	**>1 area**	**Total**
Extinct	**Observed**	23	11	34
	Expected	21.2	12.8	
Survive	**Observed**	5	6	11
	Expected	6.8	4.2	
Total		28	17	45

Table 6.25: *Analysis of extinction patterns with respect to area for* lundgreni *Zone Monograptinae, including faunas with isolated graptoloids. As expected numbers were too small to use chi-squared, the exact formula for 2x2 tables was used. p > 0.05, therefore the null hypothesis is not rejected.*

		Number of species		
		1 area	**>1 area**	**Total**
Extinct	**Observed**	16	10	26
	Expected	15.2	10.8	
Survive	**Observed**	5	5	10
	Expected	5.8	4.2	
Total		21	15	36

Table 6.26: *Analysis of extinction patterns with respect to area for* lundgreni *Zone Monograptinae, excluding faunas with isolated graptoloids. As expected numbers were too small to use chi-squared, the exact formula for 2x2 tables was used.* $p > 0.05$*, therefore the null hypothesis is not rejected.*

		Number of species		
		1 area	**>1 area**	**Total**
Extinct	**Observed**	16	5	21
	Expected	14.2	6.8	
Survive	**Observed**	5	5	10
	Expected	6.8	3.2	
Total		21	10	31

For all *lundgreni* Zone graptoloids the data are statistically significant whether or not faunas with isolated graptoloids are included (Tables 6.27 and 6.28). As has already been shown, the size of the geographical range of a species does affect extinction probability for the Retiolitidae but not for the Monograptidae. Thus, when considering *lundgreni* Zone graptoloids as a whole, the lack of significance for the Monograptidae is masked by the significance for the Retiolitidae. This illustrates the importance of analysing the data at different taxonomic levels.

Table 6.27: *Analysis of extinction patterns with respect to area for all* lundgreni *Zone graptoloids, including faunas with isolated graptoloids. Chi-squared = 4.02, with one degree of freedom.* $p < 0.05$*, therefore the null hypothesis is rejected.*

		Number of species		
		1 area	**>1 area**	**Total**
Extinct	**Observed**	36	21	57
	Expected	32.25	24.75	
Survive	**Observed**	7	12	19
	Expected	10.75	8.25	
Total		43	33	76

Table 6.28: *Analysis of extinction patterns with respect to area for all* lundgreni *Zone graptoloids, excluding faunas with isolated graptoloids. Chi-squared = 5.7, with one degree of freedom.* $p < 0.05$*, therefore the null hypothesis is rejected.*

		Number of species		
		1 area	**>1 area**	**Total**
Extinct	**Observed**	28	14	42
	Expected	23.8	18.2	
Survive	**Observed**	6	12	18
	Expected	10.2	7.8	
Total		34	26	60

6.2.3 Rarity

Rarity is often cited as a factor that makes species vulnerable to extinction (McKinney 1995, 2001). Rarity can mean low density or occurrence in a localized geographical range (McKinney 2001), but abundance and geographical range tend to be correlated; species that occur only in a small area also tend to have low abundance (Buzas & Calver 2001; McKinney 2001). The meaning discussed here is that of low density. If this holds for graptoloids at the *lundgreni* event, common species should be more likely to survive than rare ones. Testing this hypothesis in graptolites is difficult, for three reasons. Firstly, graptolite assemblages are usually time-averaged, secondly, there are problems with taphonomic and collector bias, and thirdly, data on graptolite abundances is difficult to find in the literature.

Time-averaging would not be a problem in graptolite studies if dead graptolites did not accumulate on the sea floor. Unfortunately the time that graptolite periderm would survive on the sea floor is unknown. Decay experiments on the extant pterobranch *Rhabdopleura* revealed that periderm could survive for months (Briggs *et al.* 1995), but the authors gave no upper limit for the time pterobranch skeletons could survive without being buried. Sedimentological studies by Piper (1975) in the Lake District showed that "graptolite preservation was favoured by rapid burial." If graptolites were only preserved when rapidly buried, this would mean that dead graptoloids did not survive long on the sea floor, and hence that preserved graptoloid assemblages represent a reasonably instantaneous sample rather than a time-averaged one. However, graptoloids are frequently found in hemipelagite deposits, where deposition is slow, and so obviously fast deposition is not a requirement for graptoloids to be preserved. This is an area where further taphonomic experimentation would be useful.

The second problem, that of taphonomic and collecting bias, is likely to be more of a difficulty. Some species may be more common in the preserved assemblage than they were in the living community. For example, large distinctive species may be more likely to be recognised in assemblages than small nondescript ones, because only a small part of their rhabdosome needs to be preserved, whereas for the smaller species the entire rhabdosome has to be preserved. Also, species may differ in their preservation potential – species with thicker periderm may have broken down less quickly than those with thinner periderm, and hence may be more likely to be preserved. Furthermore, some taxa, such as retiolitids and small slender monograptids, are more likely to be overlooked while collecting than large robust monograptids. All these factors will tend to bias described assemblages towards large robust monograptids with thick periderm. These species will appear more common than they actually were in life, whereas small slender graptoloids, particularly retiolitids, will appear less common. A further taxonomic bias exists in that is it possible that all species that are found as fossils are ones which were common during life, and the rare species have never been found or never been described as separate species (McKinney 1997). Rare species in graptoloids may have been described under open nomenclature.

Although exact graptoloid abundances are rarely recorded, some qualitative data does exist. Data from the Welsh Borderland, Central Asia and Nevada are discussed below.

From my work in the Welsh Borderland (see Chapter 3), *Monograptus flemingii* and *Pristiograptus dubius* are extremely common species, with *Cyrtograptus* and *Monoclimacis flumendosae* being rarer. *P. dubius* survives the *lundgreni* event; *M. flemingii* also survives, but in only a few locations. *Cyrtograptus* (with the exception of one species, found only in Australia) and *Monoclimacis flumendosae* become extinct.

Koren' (1992) and Koren' & Suyarkova (1994) give approximate species abundances ("rare", "quite numerous" or "abundant") for four sections in the Alai Range, central Asia. For all the sections, in the *lundgreni* Zone almost all species are "rare." The exceptions are *Pristiograptus dubius*, which is abundant at the top of the *lundgreni* Zone in three of the four sections. *Cometograptus nevadensis* is listed as being "quite numerous" some distance below the top of the *lundgreni* Zone, but "rare" at the top of the zone. In one section, *Testograptus testis* is shown as being "quite numerous." *Gothograptus nassa* becomes "abundant" at the top of the *lundgreni* Zone, and remains so through the *nassa-dubius* Zone. Of the species that are shown as being "quite numerous," *T. testis* becomes extinct (although it survives the event in Australia), *Com. nevadensis, P. dubius* and *G. nassa* survive.

Berry & Murphy (1975) reported that *Testograptus testis* is "particularly abundant in the [*lundgreni*] Zone and commonly occurs in marked abundance in comparison with the other members of the Zone fauna" in central Nevada. Thus, in this area, an extremely common species goes extinct.

From this data, it appears that some common species become extinct and some survive, and some rare species survive. Thus rarity does not seem to affect extinction probability, but better data are needed. Studies on the relative frequency of graptoloid species in preserved assemblages are required in order to properly address this issue.

6.2.4 Latitudinal variations in extinction patterns

Examining latitudinal patterns in extinction events can give clues as to the cause(s) of the event. If more species at high latitudes become extinct than those at low latitudes, this implies that warming may have been a causal factor in the extinction. Conversely, if more species at low latitudes become extinct, cooling may have been significant. If species after the extinction tend to be clustered around the equator, cooling may have occurred; if species are found at high latitude, warming may have taken place.

Figure 6.19 shows the localities where species survive from the *lundgreni* Zone into either the *parvus-nassa* or the *ludensis s.l.* Zone. Figure 6.20 shows the same, but excluding occurrences of *Gothograptus nassa, Pristiograptus dubius, P. parvus* and *Colonograptus deubeli*. These species have been excluded because they are widespread, and only species with a restricted distribution are required for this part

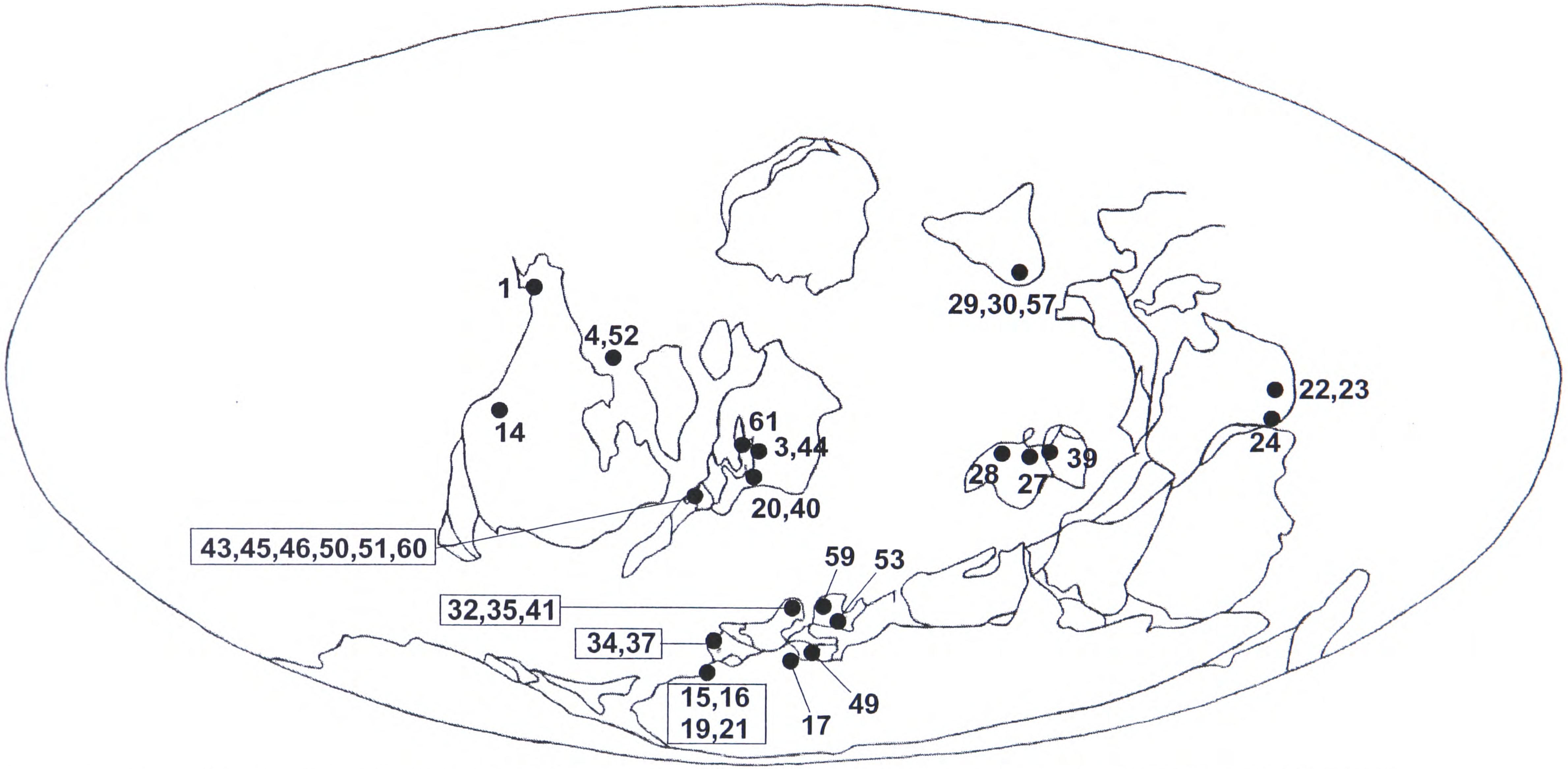


Figure 6.19: *Localities where species survive from the* lundgreni *Zone into the* parvus-nassa *or* ludensis s.l. *zones, including occurrences of* Gothograptus nassa, Pristiograptus dubius, P. parvus *and* Colonograptus deubeli. *Numbers are those of the references in Appendix 1. Map redrawn from the Paleomap website (www.scotese.com).*

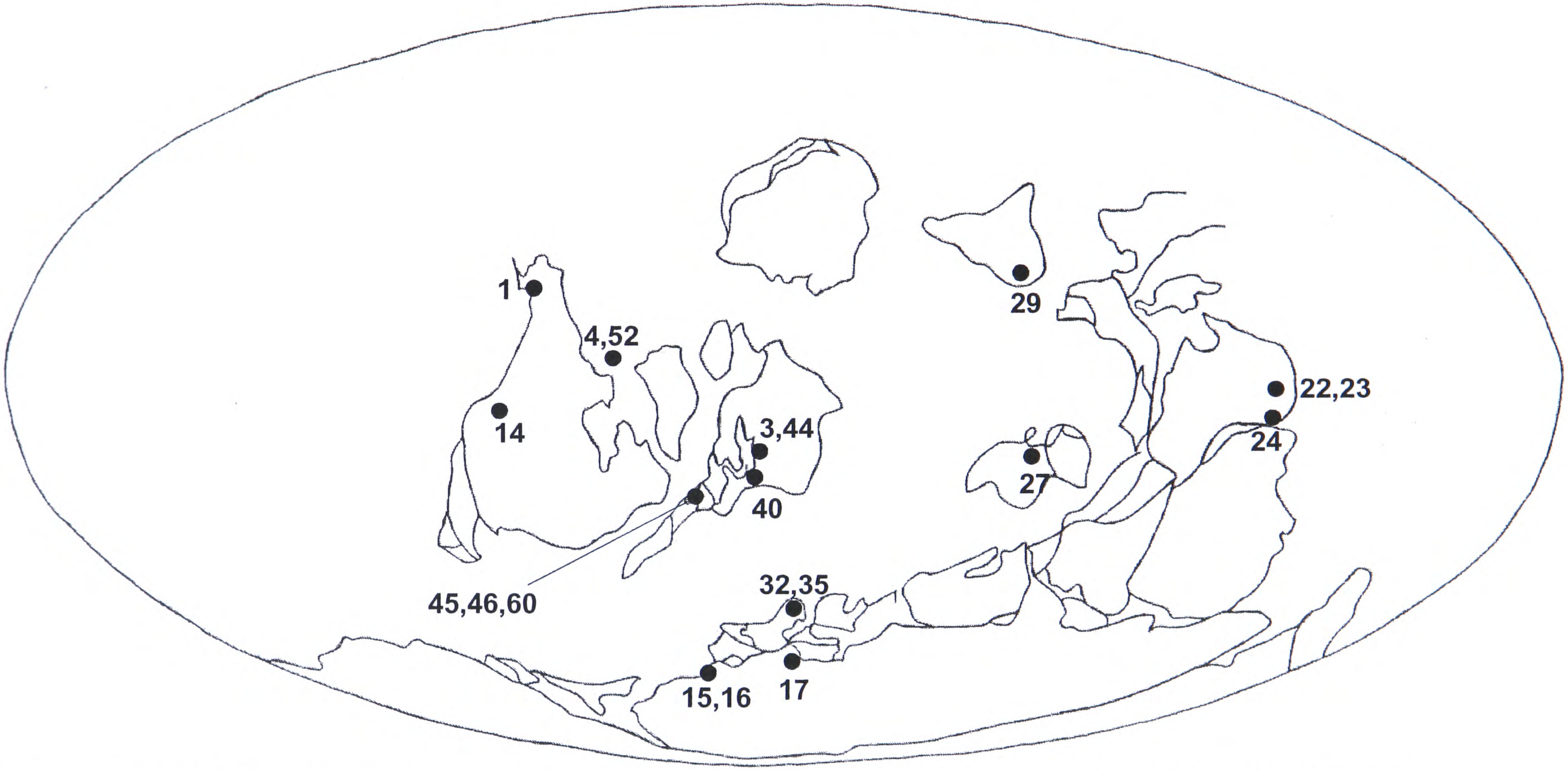


Figure 6.20: *Localities where species survive from the* lundgreni *Zone into the* parvus-nassa *or* ludensis s.l. *zones, excluding occurrences of* Gothograptus nassa, Pristiograptus dubius, P. parvus *and* Colonograptus deubeli. *Numbers are those of the references in Appendix 1. Map redrawn from the Paleomap website (www.scotese.com).*

of the study. The figures show that graptoloids after the *lundgreni* event are found both near and away from the equator; hence temperature is unlikely to have been significant in causing the *lundgreni* event.

Most, organisms show a latitudinal gradient in diversity – diversity is greatest near the equator and declines towards the poles (Rosenzweig 1995 p.25). This is seen both in the Recent and in the fossil record (Rosenzweig 1995 p.28). Thus, a latitudinal gradient in graptoloid diversity would be expected. However, no attempt has been made to see whether or not there was a latitudinal gradient in graptoloid diversity before and after the *lundgreni* event, because it is impossible to separate the real pattern from sampling bias. The reason for this is that there are many more graptoloid-bearing localities known from around the palaeo-equator than from northern and southern regions (Figure 6.7). In general, the number of species found depends on the number of sites sampled – sampling more localities means finding more species. Because of this, more species will be found near the equator than in northern and southern regions simply because there are more sites there for study. The presence of a latitudinal diversity gradient cannot be disentangled from sampling bias in this instance. Further study of graptoloid faunas away from the palaeo-equator, particularly North African and Siberian faunas, would reduce this sampling bias.

6.2.5 K- and r-selection

"An r-strategist is an organism, the life history of which is adapted to maximize its reproductive rate. A K-strategist is an organism, the life history of which is adapted to maximize its competitiveness and adult survival" (Skelton 1993 p.365). There is some work suggesting that, at times of environmental change, K-selected species are more vulnerable to extinction than r-selected ones (Chiba 1998). Table 6.29 gives a list of characteristics of K- and r-strategists; most of them not recognisable in the fossil record. Although the K/r dichotomy is somewhat crude, and does not apply to many species (Skelton 1993 p.366), it does offer a means of approach to the problem of elucidating the ecology of individual graptoloid species. There are two potential ways of telling whether or not graptoloid species were K- or r-selected: rhabdosome size and population structure.

Table 6.29: *Characteristics of K- and r-strategists (from Skelton 1993 p.366).*

K-strategists	**r-strategists**
Habitat: stable, favourable to growth and survival.	Habitat: unstable, harsh
Slow development	Rapid development
Large adult body size	Small adult body size
Late first reproduction	Early first reproduction
Iteroparity (reproduces many times)	Semelparity (reproduces once)
Few progeny per breeding episode	Many progeny per breeding episode
Long lifespan	Short lifespan
Long generation time	Short generation time

The method of looking at rhabdosome size is not as straightforward as it might appear. Species with large rhabdosomes are likely to be K-selected, those with small ones likely to be r-selected. However, there is the problem of defining what is a small rhabdosome – at what length does a small rhabdosome become a large one? In the monograptids, the species that survive tend to be small, for example *Pristiograptus parvus*, and those that become extinct tend to be larger, for example *Monoclimacis flumendosae*.

The second way of distinguishing r- from K-selected taxa is to use survivorship curves. Because K-selected taxa have low juvenile mortality and r-selected taxa have high juvenile mortality, they should have a convex survivorship curve; r-selected taxa a concave one (see Figure 6.21). The survivorship curve method could be applied to organisms other than graptoloids; any organism where some proxy for age is present on its skeleton is suitable, for example brachiopods and bivalves (growth lines), and cephalopods (septae). In graptoloids, the number of thecae is used as a proxy for age. This assumes that growth rates are the same for all individuals within a species. (Growth rates in invertebrates can vary with age (Hallam 1972), so the number of thecae may not vary linearly with age. This does not matter, as long as, within a species, an individual with x thecae is older than one with (x-1) thecae.) Different species may have had different growth rates, so this method cannot be used to compare the ages of individuals of different species.

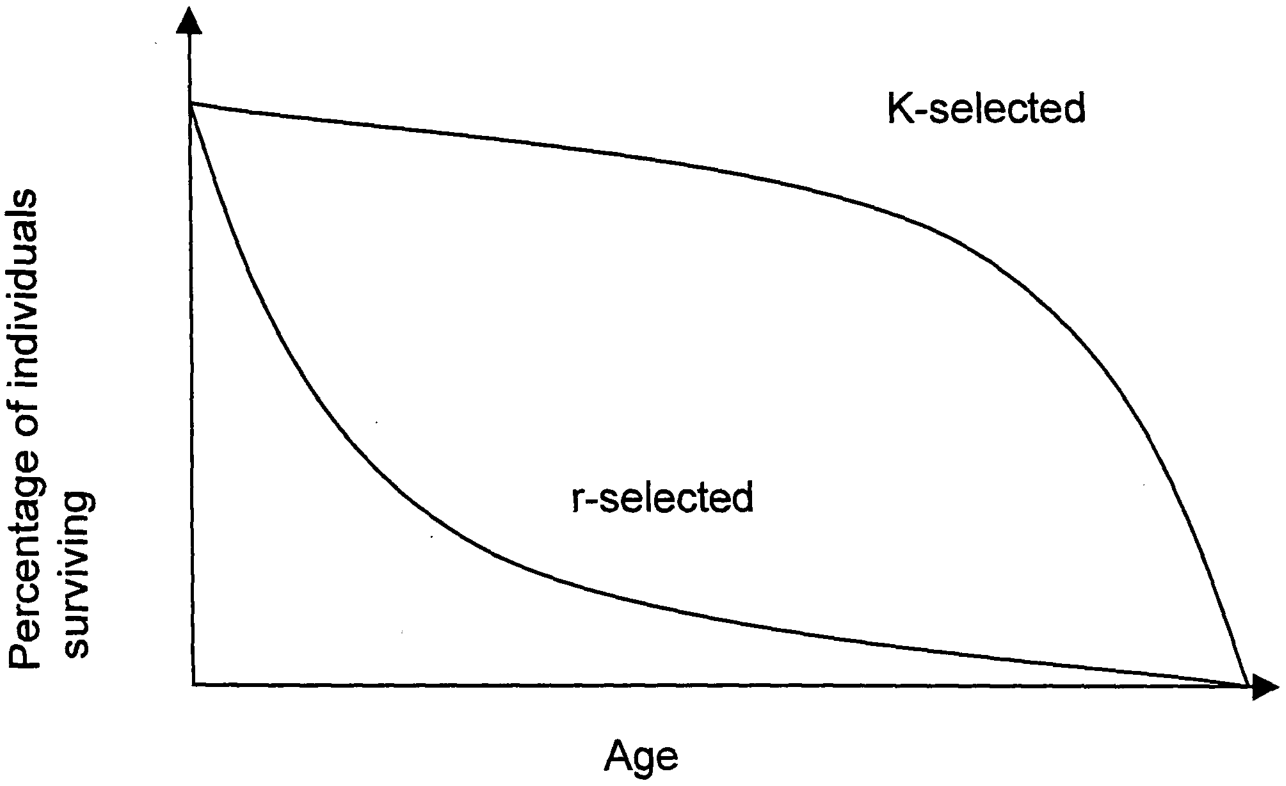


Figure 6.21: *Idealised survivorship curves. The y-axis is plotted on a logarithmic scale.*

One problem with this method is getting hold of the material to construct a survivorship curve. Unbiased collections are needed – obviously if there has been collector bias towards large or small specimens this will bias the resulting survivorship curve. Also, large collections are required in order to achieve reliable results; ideally with multiple samples from the same bed.

I have been able to use construct a survivorship curve for only one species, *Testograptus testis*. During November 2000 I collected many specimens of this species from Wallace Creek, New South Wales (see Chapter 4). I was fortunate enough to be able to return to the same outcrop in July 2002, on a field trip after the International Palaeontological Congress in Australia. On both occasions I collected every specimen I saw, thus I have two unbiased samples from the same locality. In addition, I used material collected by Chris Jenkins from Wallace Creek (Jenkins localities U4, BF50 and G12). The Jenkins sample appeared to be unbiased, because it was large (21 specimens), and contained a range of sizes, including some very small specimens.

Figure 6.22 shows the frequency of different sizes of individuals for the two samples from Wallace Creek and the sample from Chris Jenkins' collection, plotted separately. The chart shows that the two samples from Wallace Creek have the same population structure, and the Chris Jenkins sample is slightly different, the average size of graptoloids from this collection being slightly larger. The two populations have the same type of distribution, the Chris Jenkins sample being displaced to the right relative to the Wallace Creek samples.

Figure 6.23 is the survivorship curve for *Testograptus testis*. The curve is very strongly convex, which implies that *T. testis* was K-selected. Before the *lundgreni* event, *T. testis* was a common cosmopolitan species. After the *lundgreni* event, it is found only in Australia. It does not, as far as is known, have any descendants. Therefore it is fair to say that *T. testis* was severely affected by the *lundgreni* event. This supports the hypothesis that K-selected species are vulnerable to extinction. Of course, this is only one species and more data, on many more species, are needed.

6.3 Conclusions

It appears that different factors controlled the extinction of monograptids and retiolitids, which may reflect different ecologies of monograptids and retiolitids. For retiolitids, extinction vulnerability appears to have been correlated with geographic range, whereas for monograptids some genera were more vulnerable than others, which may have been due to differing life history strategies. The different controls on extinction vulnerability for monograptids and retiolitids might possibly be due to the two groups of graptoloids occupying different ecological niches. Rarity does not appear to have been a risk factor for extinction, but it is impossible to be certain with the extremely limited data available – it is possible that only common species have been recognised in the fossil record. No latitudinal bias in extinction was detected, therefore temperature is unlikely to have been significant in causing the *lundgreni* event.

Figure 6.22: *Frequency distribution of* Testograptus testis *individuals in my collection and Jenkins' collection*

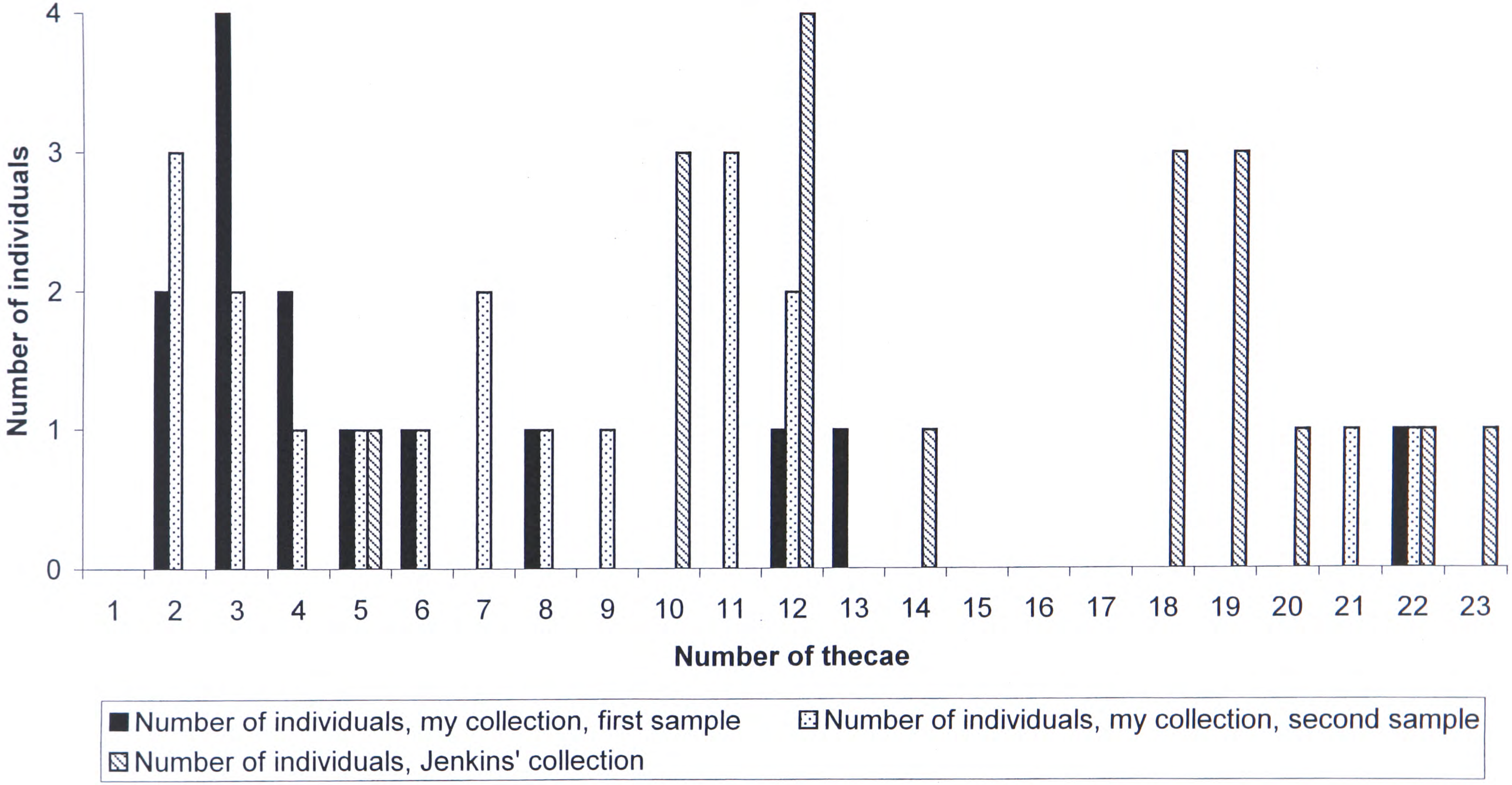
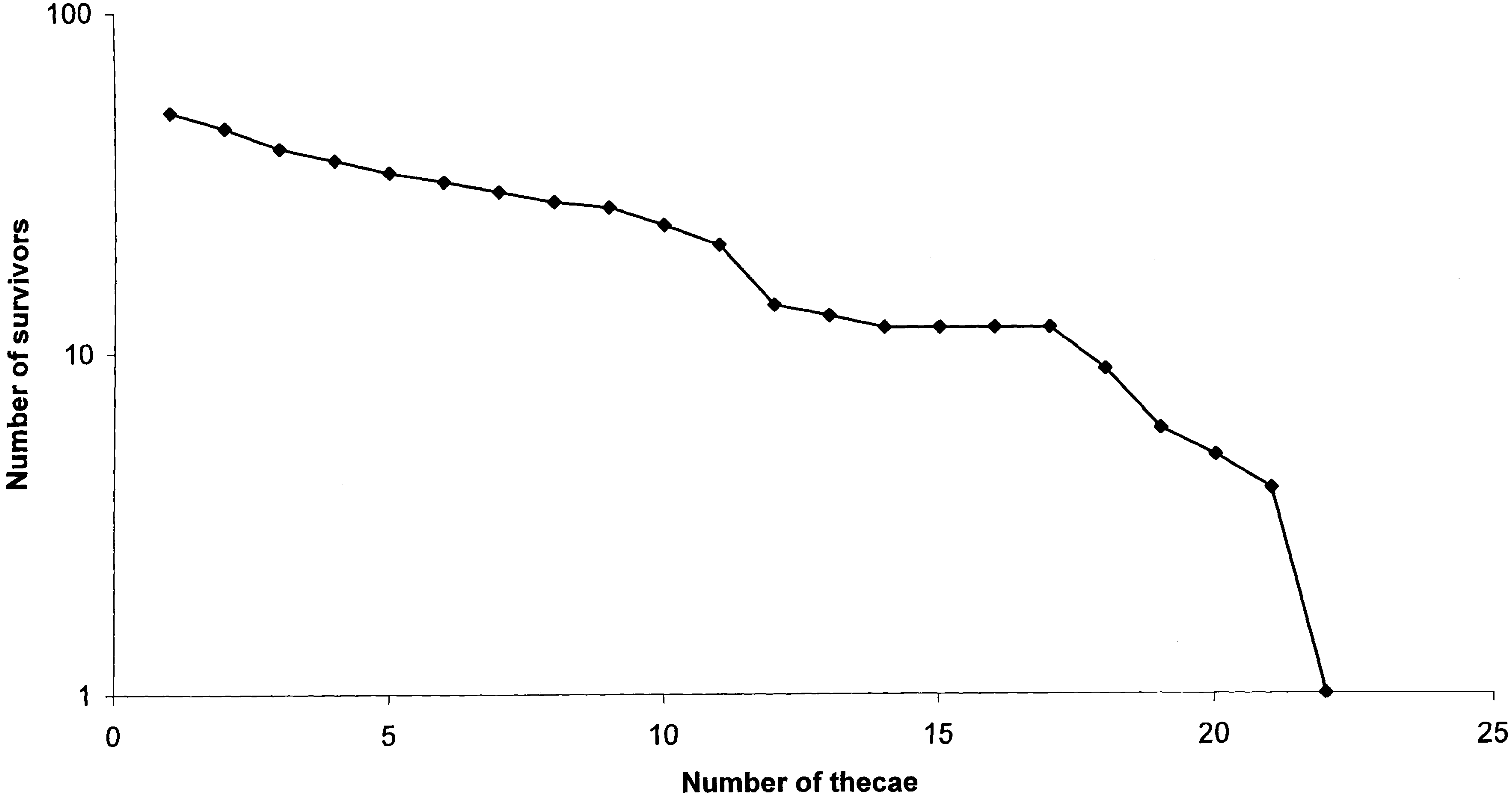


Figure 6.23: *Survivorship curve for* Testograptus testis.



7. Discussion, conclusions and suggestions for further work

7.1 Discussion and conclusions

The *lundgreni* extinction event was one of the most severe to have affected graptoloids during the Silurian. It shares similarities with some other extinction events in that it occurs during a time of sea-level fall, large taxa with complex morphologies become extinct and survivors are small taxa with simple morphology. A global literature survey of pre- and post-extinction faunas has revealed a much greater diversity immediately after the extinction than has been previously suspected. As most of the species present shortly after the extinction event occur in only one or a few localities, a true picture of the actual diversity present can only be gained from taking a global view. Survivors of the extinction are generally not widespread geographically, with the exceptions of *Gothograptus nassa, Pristiograptus dubius* and *P. parvus*. In some areas these species occur in great abundance during the *parvus-nassa* Zone (e.g. Germany, Jaeger 1991), and possibly represent disaster taxa.

A study of the amount of endemism in the faunas (Section 6.1.1) revealed that percentage endemism during the *lundgreni* Zone is lowest for the cyrtograptids, which were the group most severely affected by the extinction. This was surprising, as it was expected that the groups with highest endemism would be worst affected by the event. (It is generally considered that a species that inhabits a larger geographic area is more likely to survive a crisis than one that occurs in a smaller one, because in the larger area there is more chance of their being some place where conditions remain favourable for the species.) For the retiolitids and monograptids, there is a peak in endemism during the *parvus-nassa* Zone. Analysis of the number of species surviving from zone to zone revealed that, if a species survived into the *parvus-nassa* Zone, it had a high chance of surviving into the *ludensis* Zone *s.l.* Thus it appears that many species survived the extinction event in restricted areas, from where they spread out during the *ludensis* Zone *s.l.* There appears to have been no single refugium for all species; species are found in all areas in the *parvus-nassa* Zone, but most species are found at only one locality. Thus it appears that, although individual species had restricted distributions after the *lundgreni* event, graptoloids as a group were not restricted in their distribution. The reason why one species survived in one area and another species in a different area probably has to do with the ecology of individual species, and is beyond the scope of this work.

Analysis of the global literature indicates that graptoloid extinction is random at the family and subfamily level, i.e. the species in any family or subfamily were just as likely to survive as the species in any other family or subfamily. For the monograptids, extinction appears to be non-random at the genus level (although this could not be tested statistically), with a higher proportion of species surviving the extinction for *Pristiograptus* than for other genera.

This indicates that something about being a pristiograptid meant a greater chance of surviving extinctions. Pristiograptids are no more widespread than other species (many *lundgreni* Zone species are cosmopolitan, including victims of the extinction). Species of pristiograptid that survive the *lundgreni* event occur in both shallow and deep water (Section 2.6), so depth stratification is not involved in this. It is possible that pristiograptids ate different things from other graptoloids, and that their food supply was not affected by whatever caused the *lundgreni* event whereas the foodstuffs of other graptoloids were. Whether pristiograptids had a different diet could possibly be tested using carbon isotopes: animals have the same carbon isotope ratio as their foodstuffs (Libes 1992 p.579), and it is possible to measure carbon isotope ratios in graptolite periderm (LoDuca & Pratt 2002). Thus different carbon isotope ratios in different graptoloid species would indicate different diets.

As pristiograptids tend to be small compared to other monograptids, it is possible that they were r-selected whereas other species, victims of the event, were K-selected (Section 6.2.5). Unfortunately it was not possible to test this for a pristiograptid, due to lack of specimens. However, it was possible to determine life history strategy for one species, *Testograptus testis*. This species is K- selected and a victim of the *lundgreni* event. (Although it did not become extinct entirely at the end of the *lundgreni* Zone, it is only known from Australia after the event.) From this, admittedly limited, evidence, it appears that life history strategy is important in determining which species survived the extinction event; K-selected species being more likely to become extinct than r-selected ones. This hypothesis could be tested by determining life history strategy for both victims and survivors of the event using the method of survivorship curves described in Section 6.2.5.

From the above, aspects of graptoloid ecology appear to have been important in determining which species became extinct. It is therefore important to obtain a better understanding of the ecology of graptoloids, both of the entire group and the ecological differences between species.

Extinction likelihood does not appear to be linked with geographical distribution for monograptids. However, for retiolitids, those species with restricted ranges were more likely to become extinct than those with wide ranges. This was the case both including and excluding faunas with isolatable graptoloids, so this is not a result of monographic bias. Why geographical distribution was a factor in retiolitid extinction but not monograptid is unknown, but is probably due to the differing ecology of the two groups.

Rarity (defined as low abundance of individuals, usually correlated with a narrow geographical range) does not seem to have been a risk factor for extinction, but it is impossible to be certain with the extremely limited data available. In particular, there is virtually no data on retiolitids (Section 6.2.3). No latitudinal bias in extinction was detected, therefore temperature change is unlikely to have been significant in causing the *lundgreni* event.

Because the *lundgreni* event is similar to other extinction events, elucidation of the cause or causes of this extinction could also shed light on the cause or causes of other events. Various hypotheses for the cause of the event have been proposed: bolide impact, sea level change, expansion of anoxia, retreat of anoxia and changes in nutrient levels (Jeppsson's primo-secundo model, see section 2.7.5 for details). The hypothesis of bolide impact has been discussed fully in Chapter 2 and does not need to be mentioned further. The results of fieldwork in the Welsh Borderland and Australia are relevant to discussing some of these ideas.

The hypothesis of Quinby-Hunt & Berry (1991) that expansion of anoxia in the oceans was the cause of the *lundgreni* event is not supported by the results of fieldwork in the Welsh Borderland (Chapter 3). This study discovered that, at the time of the extinction, conditions at the sea floor changed from anoxic to oxygenated, the exact opposite of the prediction of this hypothesis. This result is consistent with the hypothesis that the retreat of anoxia was responsible (Koren' 1987; Štorch 1995), but does not prove that this was the cause. However, results from Australian fieldwork did not find any significant sedimentological change at the end of the *lundgreni* Zone (Chapter 4). In contrast with other areas, there is no regression in Australia at the end of the *lundgreni* Zone (Talent 1989), which could account for the apparent lack of sedimentological change. This absence of regression may have something to do with Australia acting as a refugium for some taxa – possibly conditions did not change as much as in other areas. Some areas of the world do show sedimentological changes at this level, but some do not (Section 2.8), which implies that changes in anoxia may not have been significant globally. Unfortunately, previous studies of sections across the *lundgreni* event have not included environmental interpretations, so it is not possible to say how environmental conditions changed at the time of the event globally. Further work on many sections around the world is needed in order to test these hypotheses.

Geochemical evidence implies elevated primary productivity after the end of the *lundgreni* Zone. This does not agree with the Jeppsson model, which predicts a fall in primary productivity at this time (Jeppsson & Calner 2003), but is in agreement with other workers who correlate increases in primary productivity with decreases in diversity. The increase in nutrients may have resulted from an increase in continental runoff, because of a greater continental area exposed during the regression that occurred in most areas at the end of the *lundgreni* Zone. Sea level change may have made the event appear more severe than it actually was, because of taphonomic effects – as was suggested by Urbanek (1993), graptoloids may have survived the extinction in the open ocean, where they were not preserved in the fossil record. This idea could be contradicted by the lack of Lazarus taxa (six were present in the global literature survey, section 6.1) – if graptoloids did survive the extinction in the open ocean, many Lazarus taxa would be expected. However, it is possible that evolution occurred in the ocean such that the descendants of the original migrants are a different species. If this is the case, Lazarus taxa can only be identified by looking at species lineages. In particular, those species with a cryptogenic origin, such as *Monograptus insperatus*, may represent Lazarus lineages.

Although it was not the aim of this work to elucidate the causes of the *lundgreni* event, it is possible to say something about them. The event is correlated with changes in sea level and nutrient levels. The change in sea level may have caused the change in nutrient levels by changing upwelling patterns and allowing increased continental runoff. Increased nutrient levels would mean increased primary productivity. In modern systems, increased productivity is correlated with decreased diversity (except at very low productivities), although the reasons for this are unclear. The relationship does appear to hold for large areas and geological timescales (Section 2.7.4). Thus the fall in diversity at the end of the *lundgreni* Zone could have resulted from an increase in primary productivity. This hypothesis could be tested by measuring palaeoproductivity, using means such as carbon and barium isotopes in areas of high and low graptoloid diversity. If this hypothesis is correct, areas of high productivity and very low productivity should be low diversity, and medium productivity higher diversity.

The mass occurrences of some species (*Gothograptus nassa, Pristiograptus dubius* and *P. parvus*) during the *parvus-nassa* Zone could reflect high abundance of plankton resulting from elevated productivity. This assumes that abundance of fossils is correlated with abundance during life. Alternatively, these mass occurrences could be taphonomic; a result of lower sedimentation rates. This could be tested by looking at the relative abundances of graptoloids and some other taxon. If the abundances of all taxa increase, then the increased abundance is probably due to sedimentological concentration. If the abundances of graptoloids only increase, this is probably due to more graptoloids being present during life.

7.2 Suggestions for further work

1. Sedimentological and geochemical analyses of sections across the *lundgreni* event would enable further testing of the hypotheses that retreat of anoxia or expansion of anoxia were responsible for the extinction. Sulphur isotopes and the size of pyrite framboids can be used in addition to sedimentology to establish the presence of anoxia (Hallam & Wignall 1997 p21; Wignall & Newton 1998).
2. Studies of palaeoproductivity together with the graptoloid faunas would enable the relative timing of the extinction and the increase in productivity to be ascertained. Clearly if the increase in productivity occurs after the extinction, the cause of the extinction was not the productivity increase.
3. Whether or not species were declining in numbers before the extinction could be determined using statistical analyses of graptoloid populations in the time leading up to the extinction.
4. Construction of survivorship curves for victims and survivors of the event would make it possible to test the hypothesis that victims were K-selected whereas survivors were r-selected. The mass occurrences of *Gothograptus nassa, Pristiograptus dubius* and *P. parvus* would be ideal subjects for this; these species should, according to the hypothesis, be r-selected. This method is also applicable to other taxa, such as molluscs and brachiopods. Both this and the preceding suggestion require large, unbiased collections.
5. The taxonomy of the *Colonograptus ludensis* group requires revision, particularly as some species in the group have been used for biostratigraphy. A statistical study of large numbers of specimens from several different localities, particularly with regard to characters that do not change during astogeny, would determine whether several species or different growth stages of one species are present. The *Pristiograptus dubius* group is also in need of taxonomic revision.

6. Graptoloid faunas from South America and Australia need to be better known; South America because it was at high latitude and hence may have different faunas and extinction patterns from other, more tropical, areas, and Australia because of its role as a refugium. The One Tree Hill section would repay further collecting, particularly because of its diverse retiolitid fauna.

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Appendix 2 Correlation of literature used in the global survey with the standard scheme.

Shaded cells indicate zones not present in the original reference. Names of zones are as given in the original references.

Reference number	n/a	1	2	3	4	5	6
Authors	Koren' *et al.* 1996	Churkin & Carter 1996	Lenz & Kozłowska-Dawidziuk 2001a	Kaljo *et al.* 1984	Lenz 1995	Lenz 1994c	Lenz 1993b
Location	Global	Alaska	Arctic Canada	Baltic region	Arctic Canada	Arctic Canada	Arctic Canada
	ludensis	*M. ludensis*		*ludensis*	*Colonograptus? ludensis*	*"Pristiograptus" ludensis*	*"Pristiograptus" ludensis*
	praedeubeli-deubeli	*M. digitatus*			*Colonograptus? praedeubeli-C? deubeli*		
	parvus-nassa			*nassa*	*Pristiograptus dubius-Gothograptus "nassa"* interval biozone		
	lundgreni	*C. lundgreni*	*lundgreni*	*testis*		*M. testis-C. lundgreni*	*Cyrtograptus lundgreni-Monograptus testis*

Reference number	n/a	7	8	9	10	11	12
Authors	Koren' *et al.* 1996	Lenz & Melchin 1990	Lenz & Melchin 1991	Lenz 1988	Lenz 1980	Bourque & Lachambre 1980	Thorsteinsson 1958
Location	Global	Arctic Canada	Arctic Canada	Northwest Territories, Canada	Northwest Territories, Canada	Quebec, Canada	Arctic Canada
	ludensis	*ludensis*	*ludensis*		"Beds with *Pristiograptus etheringtoni*"	*ludensis*	
	praedeubeli-deubeli						
	parvus-nassa						
	lundgreni	*lundgreni-testis*	*lundgreni-testis*	*Cyrtograptus lundgreni-Monograptus testis*	*testis-lundgreni*		*Monograptus testis* and *Cyrtograptus trilleri*
							Cyrtograptus lundgreni

Reference number	n/a	13	14	15	16	17	18
Authors	Koren' *et al.* 1996	Bjerreskov 1992	Berry & Murphy 1975	Bohrmann & Fischer 1985	Cornée *et al.* 1987	Jaeger *et al.* 1975	Willefert 1966
Location	Global	Greenland	Nevada, USA	Morocco	Morocco	Tunisia	Morocco
	ludensis		*Pristiograptus ludensis*	*ludensis*	*ludensis*	*Monograptus vulgaris*	
	praedeubeli-deubeli						
	parvus-nassa		*Pristiograptus dubius frequens*			"Transition Wenlock-Ludlow"	
	lundgreni	*lundgreni-testis*	*Monograptus testis*			Zone 31 – *Cyrtograptus lundgreni*	*lundgreni*

Reference number	n/a	19	20	21	22	23	24
Authors	Koren' *et al.* 1996	Lüning *et al.* 2000	Kozłowska-Dawidziuk 1999	Massa 1965	Rickards *et al.* 1995a	Rickards & Wright 1997	Rickards & Sandford 1998
Location	Global	Morocco	Poland	Algeria	New South Wales	New South Wales	Victoria
	ludensis	*ludensis*		*Beds with M. deubeli*	*ludensis*		*ludensis*
	praedeubeli-deubeli		*Colonograptus praedeubeli*			*sherrardae*	
	parvus-nassa		*dubius/nassa*				*nassa*
			dubius parvus				*parvus*
	lundgreni		*Cyrtograptus lundgreni/ Testograptus testis*	*lundgreni*	*lundgreni-testis*		*testis*

Reference number	n/a	25	26	27	28	29	30
Authors	Koren' *et al.* 1996	Jones 1973	Dean *et al.* 1999	Zhang & Lenz 1997	Lenz *et al.* 1996	Koren' 1991	Koren' & Suyarkova 1994
Location	Global	Malaysia	Turkey	China	China	Central Asia	Central Asia
	ludensis			*Colonograptus ludensis*	Upper Homerian	*ludensis*	*ludensis*
	praedeubeli-deubeli			*Colonograptus praedeubeli*		*deubeli*	*deubeli*
						sherrardae (praedeubeli)	*sherrardae (praedeubeli)*
	parvus-nassa					*nassa/dubius*	*nassa/dubius*
	lundgreni	*Cyrtograptus lundgreni*	*lundgreni*			*lundgreni/testis*	*lundgreni/testis*

Reference number	n/a	31	32	33	34	35	36
Authors	Koren’ *et al.* 1996	Paalits *et al.* 1998	Kozłowska-Dawidziuk *et al.* 2001	Kriz *et al.* 1993	Gutierrez-Marco *et al.* 1996	Jaeger 1991	Gutiérrez-Marco *et al.* 1997
Location	Global	Southern Urals	Czech Republic	Czech Republic	Spain/Portugal	Germany	Spain
	ludensis		*gerhardi-ludensis*		*ludensis*	*M. gerhardi* & *M. ludensis*	
	praedeubeli-deubeli	*praedeubeli-deubeli*	*praedeubeli-deubeli*		*praedeubeli-deubeli*	*M. deubeli* *M. praedeubeli*	
	parvus-nassa		*parvus-nassa*		*“parvus”-“nassa”*	*M. dubius/Ret. nassa* Interregnum *M. dubius parvus*	
	lundgreni			*C. lundgreni/T. testis*	*testis-lundgreni*	*Cyrtograptus lundgreni* zone, *M. testis* subzone	*lundgreni*

Reference number	n/a	37	38	39	40	41	42
Authors	Koren' *et al.* 1996	Jaeger & Robardet 1979	Bjerreskov & Jørgensen 1983	Ni 1997	Teller 1969	Štorch 1994	Maletz *et al.* 2002
Location	Global	Spain	Denmark	China	Poland	Czech Republic	Bolivia
	ludensis			Upper Homerian	*Pristiograptus vulgaris*	*ludensis*	Late Homerian
	praedeubeli-deubeli	*deubeli*				*praedeubeli-deubeli*	
	parvus-nassa	*M. dubius-G. nassa*			*Gothograptus nassa*	*nassa-frequens* *parvus*	
	lundgreni	*C. lundgreni*	*lundgreni* (probably lower part)		*Cyrtograptus lundgreni*	*lundgreni*	

Reference number	n/a	43	44	45	46	47	48
Authors	Koren' *et al.* 1996	Zalasiewicz & Williams 1999	Paškevičius 1979	Warren 1971	Holland *et al.* 1969	White *et al.* 1991	Fu 1980
Location	Global	UK	Lithuania	UK	UK	UK	China
	ludensis	*nassa-ludensis*	*Monograptus ludensis*	*Pristiograptus ludensis*	*ludensis*		
	praedeubeli-deubeli						
	parvus-nassa		*Gothograptus nassa*	*Gothograptus nassa*	*nassa/dubius* Interregnum		
	lundgreni	*lundgreni*	*Monograptus testis*	*C. lundgreni*	*lundgreni*	*C. lundgreni*	*Cyrtograptus lundgreni*

Reference number	n/a	49	50	51	52	53	54
Authors	Koren' *et al.* 1996	Barca & Jaeger 1989	Rickards 1969	Burns & Rickards 1993	Lenz & Kozłowska-Dawidziuk 2002a	Sachanski 1998	Obut *et al.* 1965
Location	Global	Italy	UK	Ireland	Arctic Canada	Bulgaria	Northern Siberia
	ludensis	▨	*ludensis*	*ludensis*	*ludensis*	*C. ludensis*	*Pristiograptus vulgaris*
	praedeubeli-deubeli	*M. deubeli* *M. praedeubeli*			*praedeubeli-deubeli*		
	parvus-nassa	*M. dubius/R. nassa* Interregnum	▨	▨	*dubius-nassa*	▨	▨
		M. dubius parvus					
	lundgreni	*lundgreni* zone, *testis* subzone	*lundgreni*	*lundgreni*	▨	*Cyrt. lundgreni*	*Monograptus testis*

Reference number	n/a	55	56	57	58	59	60
Authors	Koren' *et al.* 1996	Obut & Sobolevskaya 1966	Obut *et al.* 1967	Koren' 1992	Rinenberg 1990	Iordan 1981	Palmer 1970
Location	Global	Kazakhstan	Northeast USSR	Central Asia	Central Asia	Romania	Ireland
	ludensis			*ludensis*		*nassa-vulgaris*	*Monograptus ludensis*
	praedeubeli-deubeli			*deubeli* *sherrardae (praedeubeli)*			
	parvus-nassa			*nassa/dubius*			
	lundgreni	*Monograptus testis*	*Monograptus testis & Cyrtograptus lundgreni*	*lundgreni/testis*	*Monograptus testis*	*testis* *lundgreni*	

Reference number	n/a	61	62	63
Authors	Koren' *et al.* 1996	Jeppsson & Calner 2000	Kozłowska-Dawidziuk 1990	Kozłowska-Dawidziuk 1995
Location	Global	Sweden	Poland	Poland
	ludensis			
	praedeubeli-deubeli	*Colonograptus(?) praedeubeli*		
	parvus-nassa	*Gothograptus nassa* *Pristiograptus dubius parvus*		
	lundgreni	*M. testis*	*lundgreni*	*lundgreni*

Appendix 3 Occurrences of species in different places and zones

Shaded cells indicate that the reference did not include that particular zone. Numbers are those of the references in Appendix 1.

lundgreni Zone neoglyptograptid species

Genus	Species	Author	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Neoglyptograptus	*sussmilchi*	Rickards *et al.* 1995a				▨							▨				▨	▨

Genus	Species	Author	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Neoglyptograptus	*sussmilchi*	Rickards *et al.* 1995a			▨				▨	?			▨	▨			▨	▨

Genus	Species	Author	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Neoglyptograptus	*sussmilchi*	Rickards *et al.* 1995a							▨			▨						

Genus	Species	Author	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Neoglyptograptus	*sussmilchi*	Rickards *et al.* 1995a				▨								▨			

ludensis Zone _s.l._ neoglyptograptid species

Genus	Species	Author	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Neoglyptograptus	*sussmilchi*	Rickards *et al.* 1995a		▨							▨			▨	▨			

Genus	Species	Author	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Neoglyptograptus	*sussmilchi*	Rickards *et al.* 1995a		▨				x			▨	▨						

Genus	Species	Author	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Neoglyptograptus	*sussmilchi*	Rickards *et al.* 1995a	▨			▨		▨									▨	▨

Genus	Species	Author	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Neoglyptograptus	*sussmilchi*	Rickards *et al.* 1995a							▨	▨		▨				▨	▨

lundgreni Zone retiolitid species

Genus	Species	Author	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Plectograptus	*absimilis*	Rinenberg																
Plectograptus	*aksuensis*	Rinenberg																
Cometograptus	*apoxys*	(Lenz 1993b)		x				x										
Cometograptus	*apsis*	Lenz & Kozłowska-Dawidziuk 2001a		x														
Sagenograptus	*arctos*	Lenz & Kozłowska-Dawidziuk 2001a		x														
Retiolites	*australis*	McCoy 1875		?														
Cometograptus	*bicladis*	(Lenz 1993c)		x														
Spinograptus	*clathrospinosus*	(Eisenack 1951)						x	x									
Paraplectograptus	*eiseli*	(Manck 1917)						x	x					x				
Eisenackograptus	*eisenacki*	(Obut & Sobolevskaya in Obut *et al.* 1965)		x	cf		x	x										
Paraplectograptus	*fidelis*	Rinenberg																
Cometograptus	*kirki*	Lenz & Kozłowska-Dawidziuk 2001a		x														
Gothograptus	*kozlowskii*	Kozłowska-Dawidziuk 1990																
Sokolovograptus	*lejskoviensis*	(Bouček 1931)																
Cometograptus	*marsupium*	(Lenz 1993b)		x				x										
Paraplectograptus	*minutus*	Rickards *et al.* 1995a																
Gothograptus	*nassa*	(Holm 1890)			x													
Cometograptus	*nevadensis*	(Berry & Murphy 1975)		x			x	x	x	x						x		
Gothograptus	*obtectus*	Kozłowska-Dawidziuk 1990																
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)		?				x	x									
Gothograptus	*pseudospinosus*	Eisenack 1951			x													
Pseudoplectograptus	*sagenus*	(Lenz 1993b)		x			x	x										
Pseudoplectograptus	*simplex*	Kozłowska-Dawidziuk 1995		x														
Gothograptus	*tenuis*	(Eisenack 1951)			x													
Sokolovograptus	*textor*	(Bouček & Münch 1952)					x	x										

***lundgreni* Zone retiolitid species (continued)**

Genus	Species	Author	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Plectograptus	*absimilis*	Rinenberg																
Plectograptus	*aksuensis*	Rinenberg																
Cometograptus	*apoxys*	(Lenz 1993b)																
Cometograptus	*apsis*	Lenz & Kozłowska-Dawidziuk 2001a																
Sagenograptus	*arctos*	Lenz & Kozłowska-Dawidziuk 2001a																
Retiolites	*australis*	McCoy 1875																
Cometograptus	*bicladis*	(Lenz 1993c)																
Spinograptus	*clathrospinosus*	(Eisenack 1951)																
Paraplectograptus	*eiseli*	(Manck 1917)	x	x											x			
Eisenackograptus	*eisenacki*	(Obut & Sobolevskaya in Obut *et al.* 1965)																
Paraplectograptus	*fidelis*	Rinenberg																
Cometograptus	*kirki*	Lenz & Kozłowska-Dawidziuk 2001a																
Gothograptus	*kozlowskii*	Kozłowska-Dawidziuk 1990																
Sokolovograptus	*lejskoviensis*	(Bouček 1931)		?				x										
Cometograptus	*marsupium*	(Lenz 1993b)																
Paraplectograptus	*minutus*	Rickards *et al.* 1995a						x										
Gothograptus	*nassa*	(Holm 1890)					x	?							x	x		
Cometograptus	*nevadensis*	(Berry & Murphy 1975)																
Gothograptus	*obtectus*	Kozłowska-Dawidziuk 1990																
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)		x				x							x			
Gothograptus	*pseudospinosus*	Eisenack 1951						x										
Pseudoplectograptus	*sagenus*	(Lenz 1993b)																
Pseudoplectograptus	*simplex*	Kozłowska-Dawidziuk 1995																
Gothograptus	*tenuis*	(Eisenack 1951)																
Sokolovograptus	*textor*	(Bouček & Münch 1952)						x										

***lundgreni* Zone retiolitid species (continued)**

Genus	Species	Author	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Plectograptus	*absimilis*	Rinenberg																
Plectograptus	*aksuensis*	Rinenberg																
Cometograptus	*apoxys*	(Lenz 1993b)																
Cometograptus	*apsis*	Lenz & Kozłowska-Dawidziuk 2001a																
Sagenograptus	*arctos*	Lenz & Kozłowska-Dawidziuk 2001a																
Retiolites	*australis*	McCoy 1875																
Cometograptus	*bicladis*	(Lenz 1993c)																
Spinograptus	*clathrospinosus*	(Eisenack 1951)																
Paraplectograptus	*eiseli*	(Manck 1917)			x						x							
Eisenackograptus	*eisenacki*	(Obut & Sobolevskaya in Obut *et al.* 1965)												cf				
Paraplectograptus	*fidelis*	Rinenberg																
Cometograptus	*kirki*	Lenz & Kozłowska-Dawidziuk 2001a																
Gothograptus	*kozlowskii*	Kozłowska-Dawidziuk 1990																
Sokolovograptus	*lejskoviensis*	(Bouček 1931)																
Cometograptus	*marsupium*	(Lenz 1993b)																
Paraplectograptus	*minutus*	Rickards *et al.* 1995a																
Gothograptus	*nassa*	(Holm 1890)								x								
Cometograptus	*nevadensis*	(Berry & Murphy 1975)																
Gothograptus	*obtectus*	Kozłowska-Dawidziuk 1990																
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)									x							
Gothograptus	*pseudospinosus*	Eisenack 1951			x									x				
Pseudoplectograptus	*sagenus*	(Lenz 1993b)																
Pseudoplectograptus	*simplex*	Kozłowska-Dawidziuk 1995																
Gothograptus	*tenuis*	(Eisenack 1951)												x				
Sokolovograptus	*textor*	(Bouček & Münch 1952)												x				

***lundgreni* Zone retiolitid species (continued)**

Genus	**Species**	**Author**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**
Plectograptus	*absimilis*	Rinenberg										x					
Plectograptus	*aksuensis*	Rinenberg										x					
Cometograptus	*apoxys*	(Lenz 1993b)															
Cometograptus	*apsis*	Lenz & Kozłowska-Dawidziuk 2001a															
Sagenograptus	*arctos*	Lenz & Kozłowska-Dawidziuk 2001a															
Retiolites	*australis*	McCoy 1875															
Cometograptus	*bicladis*	(Lenz 1993c)															
Spinograptus	*clathrospinosus*	(Eisenack 1951)															
Paraplectograptus	*eiseli*	(Manck 1917)	x								x	x				x	x
Eisenackograptus	*eisenacki*	(Obut & Sobolevskaya in Obut *et al.* 1965)						x								x	x
Paraplectograptus	*fidelis*	Rinenberg										?					
Cometograptus	*kirki*	Lenz & Kozłowska-Dawidziuk 2001a															
Gothograptus	*kozlowskii*	Kozłowska-Dawidziuk 1990													x		
Sokolovograptus	*lejskoviensis*	(Bouček 1931)										x					
Cometograptus	*marsupium*	(Lenz 1993b)															
Paraplectograptus	*minutus*	Rickards *et al.* 1995a															
Gothograptus	*nassa*	(Holm 1890)									x						
Cometograptus	*nevadensis*	(Berry & Murphy 1975)									x						
Gothograptus	*obtectus*	Kozłowska-Dawidziuk 1990														x	x
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)								aff		x	cf				x
Gothograptus	*pseudospinosus*	Eisenack 1951	ex gr													x	x
Pseudoplectograptus	*sagenus*	(Lenz 1993b)															x
Pseudoplectograptus	*simplex*	Kozłowska-Dawidziuk 1995															x
Gothograptus	*tenuis*	(Eisenack 1951)						x									
Sokolovograptus	*textor*	(Bouček & Münch 1952)															

***parvus-nassa* Zone retiolitids**

Genus	Species	Author	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Spinograptus	*clathrospinosus*	(Eisenack 1951)																
Plectograptus	*dubius*	Bouček & Münch 1952																
Retiolites (Gothograptus)	*gigantonassa*																	
Gothograptus	*intermedius*	Bouček & Münch																
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)																
Sokolovograptus	*lejskoviensis*	(Bouček 1931)			x													
Gothograptus	*nassa*	(Holm 1890)			x	x										x		
Cometograptus	*nevadensis*	(Berry & Murphy 1975)																
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)			x													
Gothograptus	*pseudospinosus*	Eisenack 1951			x													
Spinograptus	*reticulolawsoni*	Kozłowska-Dawidziuk 1997																
Spinograptus	*spinosus*	(Wood 1900)														x		

Genus	Species	Author	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Spinograptus	*clathrospinosus*	(Eisenack 1951)																x
Plectograptus	*dubius*	Bouček & Münch 1952																
Retiolites (Gothograptus)	*gigantonassa*																	
Gothograptus	*intermedius*	Bouček & Münch																
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)																x
Sokolovograptus	*lejskoviensis*	(Bouček 1931)																
Gothograptus	*nassa*	(Holm 1890)	x			x				x					x	x		x
Cometograptus	*nevadensis*	(Berry & Murphy 1975)																cf
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)													x			
Gothograptus	*pseudospinosus*	Eisenack 1951																
Spinograptus	*reticulolawsoni*	Kozłowska-Dawidziuk 1997																?
Spinograptus	*spinosus*	(Wood 1900)																

parvus-nassa Zone retiolitids (continued)

Genus	Species	Author	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Spinograptus	*clathrospinosus*	(Eisenack 1951)																
Plectograptus	*dubius*	Bouček & Münch 1952													aff?			
Retiolites (Gothograptus)	*gigantonassa*				x													
Gothograptus	*intermedius*	Bouček & Münch													x			
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)																
Sokolovograptus	*lejskoviensis*	(Bouček 1931)																
Gothograptus	*nassa*	(Holm 1890)		x	x		x			x	x			x	x	x		
Cometograptus	*nevadensis*	(Berry & Murphy 1975)																
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)												x				
Gothograptus	*pseudospinosus*	Eisenack 1951																
Spinograptus	*reticulolawsoni*	Kozłowska-Dawidziuk 1997																
Spinograptus	*spinosus*	(Wood 1900)																

Genus	Species	Author	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Spinograptus	*clathrospinosus*	(Eisenack 1951)															
Plectograptus	*dubius*	Bouček & Münch 1952															
Retiolites (Gothograptus)	*gigantonassa*																
Gothograptus	*intermedius*	Bouček & Münch															
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)															
Sokolovograptus	*lejskoviensis*	(Bouček 1931)															
Gothograptus	*nassa*	(Holm 1890)	x			x									x		
Cometograptus	*nevadensis*	(Berry & Murphy 1975)															
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)															
Gothograptus	*pseudospinosus*	Eisenack 1951															
Spinograptus	*reticulolawsoni*	Kozłowska-Dawidziuk 1997															
Spinograptus	*spinosus*	(Wood 1900)															

ludensis Zone *s.l.* retiolitid species

Genus	Species	Author	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Baculograptus	*batesi*	Lenz & Kozłowska-Dawidziuk 2002a																
Baculograptus	*chainos*	(Lenz 1993b)				x												
Spinograptus	*clathrospinosus*	(Eisenack 1951)				x												
Retiolites (Gothograptus)	*eximinassa*																	
Retiolites (Gothograptus)	*gigantonassa*																	
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)																
Spinograptus	*latespinosus*	Kozłowska-Dawidziuk 1997																
Doliograptus	*latus*	Lenz & Kozłowska-Dawidziuk 2002a																
Spinograptus	*lawsoni*	(Holland, Rickards & Warren 1969)	cf															
Plectograptus	*macilentus*	(Törnquist 1887)				x												
Cometograptus	*marsupium*	(Lenz 1993b)																
Spinograptus	*munchi*	(Eisenack 1951)																
Gothograptus	*nassa*	(Holm 1890)			x											x		x
Cometograptus	*nevadensis*	(Berry & Murphy 1975)	cf			x												
Plectograptus?	*ovatus*	Kozłowska-Dawidziuk, Lenz & Štorch 2001																
Papiliograptus	*papilio*	Lenz & Kozłowska-Dawidziuk 2002a																
Papiliograptus?	*petilus*	Lenz & Kozłowska-Dawidziuk 2002a																
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)																
Spinograptus	*praerobustus*	Lenz & Kozłowska-Dawidziuk 2002a																
Gothograptus	*pseudospinosus*	Eisenack 1951																
Spinograptus	*reticulolawsoni*	Kozłowska-Dawidziuk 1997																
Plectograptus	*robustus*	(Obut & Zaslavskaya 1983)				x												
Spinograptus	*spinosus*	(Wood 1900)														x		
Sokolovograptus	*textor*	(Bouček & Münch 1952)																
Plectograptus	*wimani*	(Eisenack 1951)				?												

***ludensis* Zone *s.l.* retiolitid species (continued)**

Genus	Species	Author	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Baculograptus	*batesi*	Lenz & Kozłowska-Dawidziuk 2002a																
Baculograptus	*chainos*	(Lenz 1993b)							x									
Spinograptus	*clathrospinosus*	(Eisenack 1951)	cf					x					x					x
Retiolites (Gothograptus)	*eximinassa*																	
Retiolites (Gothograptus)	*gigantonassa*																	
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)																x
Spinograptus	*latespinosus*	Kozłowska-Dawidziuk 1997				x												
Doliograptus	*latus*	Lenz & Kozłowska-Dawidziuk 2002a																
Spinograptus	*lawsoni*	(Holland, Rickards & Warren 1969)																
Plectograptus	*macilentus*	(Törnquist 1887)												x				x
Cometograptus	*marsupium*	(Lenz 1993b)							x									
Spinograptus	*munchi*	(Eisenack 1951)						x										x
Gothograptus	*nassa*	(Holm 1890)						x					x	x	x	x		x
Cometograptus	*nevadensis*	(Berry & Murphy 1975)																
Plectograptus?	*ovatus*	Kozłowska-Dawidziuk, Lenz & Štorch 2001																x
Papiliograptus	*papilio*	Lenz & Kozłowska-Dawidziuk 2002a																
Papiliograptus?	*petilus*	Lenz & Kozłowska-Dawidziuk 2002a																
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)						x							x			
Spinograptus	*praerobustus*	Lenz & Kozłowska-Dawidziuk 2002a																
Gothograptus	*pseudospinosus*	Eisenack 1951						x										
Spinograptus	*reticulolawsoni*	Kozłowska-Dawidziuk 1997				x												
Plectograptus	*robustus*	(Obut & Zaslavskaya 1983)						x								x		
Spinograptus	*spinosus*	(Wood 1900)																
Sokolovograptus	*textor*	(Bouček & Münch 1952)																
Plectograptus	*wimani*	(Eisenack 1951)																

ludensis Zone _s.l._ retiolitid species (continued)

Genus	Species	Author	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Baculograptus	*batesi*	Lenz & Kozłowska-Dawidziuk 2002a																
Baculograptus	*chainos*	(Lenz 1993b)																
Spinograptus	*clathrospinosus*	(Eisenack 1951)			x					x								
Retiolites (Gothograptus)	*eximinassa*				x													
Retiolites (Gothograptus)	*gigantonassa*				x													
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)																
Spinograptus	*latespinosus*	Kozłowska-Dawidziuk 1997																
Doliograptus	*latus*	Lenz & Kozłowska-Dawidziuk 2002a																
Spinograptus	*lawsoni*	(Holland, Rickards & Warren 1969)														x		
Plectograptus	*macilentus*	(Törnquist 1887)			x													
Cometograptus	*marsupium*	(Lenz 1993b)																
Spinograptus	*munchi*	(Eisenack 1951)			x					x								
Gothograptus	*nassa*	(Holm 1890)		x	x		x						x	x	x	x		
Cometograptus	*nevadensis*	(Berry & Murphy 1975)																
Plectograptus?	*ovatus*	Kozłowska-Dawidziuk, Lenz & Štorch 2001																
Papiliograptus	*papilio*	Lenz & Kozłowska-Dawidziuk 2002a																
Papiliograptus?	*petilus*	Lenz & Kozłowska-Dawidziuk 2002a																
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)																
Spinograptus	*praerobustus*	Lenz & Kozłowska-Dawidziuk 2002a																
Gothograptus	*pseudospinosus*	Eisenack 1951																
Spinograptus	*reticulolawsoni*	Kozłowska-Dawidziuk 1997																
Plectograptus	*robustus*	(Obut & Zaslavskaya 1983)																
Spinograptus	*spinosus*	(Wood 1900)																
Sokolovograptus	*textor*	(Bouček & Münch 1952)							x									
Plectograptus	*wimani*	(Eisenack 1951)			cf					x								

ludensis Zone _s.l._ retiolitid species (continued)

Genus	Species	Author	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Baculograptus	*batesi*	Lenz & Kozłowska-Dawidziuk 2002a				x											
Baculograptus	*chainos*	(Lenz 1993b)				x											
Spinograptus	*clathrospinosus*	(Eisenack 1951)				x											
Retiolites (Gothograptus)	*eximinassa*																
Retiolites (Gothograptus)	*gigantonassa*																
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)				cf											
Spinograptus	*latespinosus*	Kozłowska-Dawidziuk 1997				x											
Doliograptus	*latus*	Lenz & Kozłowska-Dawidziuk 2002a				x											
Spinograptus	*lawsoni*	(Holland, Rickards & Warren 1969)															
Plectograptus	*macilentus*	(Törnquist 1887)											x				
Cometograptus	*marsupium*	(Lenz 1993b)															
Spinograptus	*munchi*	(Eisenack 1951)															
Gothograptus	*nassa*	(Holm 1890)	x	x			x				x				x		
Cometograptus	*nevadensis*	(Berry & Murphy 1975)															
Plectograptus?	*ovatus*	Kozłowska-Dawidziuk, Lenz & Štorch 2001															
Papiliograptus	*papilio*	Lenz & Kozłowska-Dawidziuk 2002a				x											
Papiliograptus?	*petilus*	Lenz & Kozłowska-Dawidziuk 2002a				x											
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)															
Spinograptus	*praerobustus*	Lenz & Kozłowska-Dawidziuk 2002a				x											
Gothograptus	*pseudospinosus*	Eisenack 1951															
Spinograptus	*reticulolawsoni*	Kozłowska-Dawidziuk 1997															
Plectograptus	*robustus*	(Obut & Zaslavskaya 1983)															
Spinograptus	*spinosus*	(Wood 1900)				x											
Sokolovograptus	*textor*	(Bouček & Münch 1952)															
Plectograptus	*wimani*	(Eisenack 1951)															

praedeubeli-deubeli Zone retiolitids

Genus	Species	Author	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Baculograptus	*batesi*	Lenz & Kozłowska-Dawidziuk 2002a																
Baculograptus	*chainos*	(Lenz 1993b)				x												
Spinograptus	*clathrospinosus*	(Eisenack 1951)				x												
Retiolites (Gothograptus)	*gigantonassa*																	
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)																
Spinograptus	*latespinosus*	Kozłowska-Dawidziuk 1997																
Doliograptus	*latus*	Lenz & Kozłowska-Dawidziuk 2002a																
Plectograptus	*macilentus*	(Törnquist 1887)				x												
Cometograptus	*marsupium*	(Lenz 1993b)																
Spinograptus	*munchi*	(Eisenack 1951)																
Gothograptus	*nassa*	(Holm 1890)																
Cometograptus	*nevadensis*	(Berry & Murphy 1975)				x												
Papiliograptus	*papilio*	Lenz & Kozłowska-Dawidziuk 2002a																
Papiliograptus?	*petilus*	Lenz & Kozłowska-Dawidziuk 2002a																
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)																
Spinograptus	*praerobustus*	Lenz & Kozłowska-Dawidziuk 2002a																
Spinograptus	*reticulolawsoni*	Kozłowska-Dawidziuk 1997																
Plectograptus	*robustus*	(Obut & Zaslavskaya 1983)				x												
Plectograptus	*wimani*	(Eisenack 1951)				?												

***praedeubeli-deubeli* Zone retiolitids (continued)**

Genus	Species	Author	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Baculograptus	*batesi*	Lenz & Kozłowska-Dawidziuk 2002a																
Baculograptus	*chainos*	(Lenz 1993b)							x									
Spinograptus	*clathrospinosus*	(Eisenack 1951)																x
Retiolites (Gothograptus)	*gigantonassa*																	
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)																x
Spinograptus	*latespinosus*	Kozłowska-Dawidziuk 1997				x												
Doliograptus	*latus*	Lenz & Kozłowska-Dawidziuk 2002a																
Plectograptus	*macilentus*	(Törnquist 1887)																
Cometograptus	*marsupium*	(Lenz 1993b)							x									
Spinograptus	*munchi*	(Eisenack 1951)																x
Gothograptus	*nassa*	(Holm 1890)													x	x		x
Cometograptus	*nevadensis*	(Berry & Murphy 1975)																
Papiliograptus	*papilio*	Lenz & Kozłowska-Dawidziuk 2002a																
Papiliograptus?	*petilus*	Lenz & Kozłowska-Dawidziuk 2002a																
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)													x			
Spinograptus	*praerobustus*	Lenz & Kozłowska-Dawidziuk 2002a																
Spinograptus	*reticulolawsoni*	Kozłowska-Dawidziuk 1997				x												
Plectograptus	*robustus*	(Obut & Zaslavskaya 1983)														x		
Plectograptus	*wimani*	(Eisenack 1951)																

praedeubeli-deubeli **Zone retiolitids (continued)**

Genus	**Species**	**Author**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**
Baculograptus	*batesi*	Lenz & Kozłowska-Dawidziuk 2002a																
Baculograptus	*chainos*	(Lenz 1993b)																
Spinograptus	*clathrospinosus*	(Eisenack 1951)			x													
Retiolites (Gothograptus)	*gigantonassa*				x													
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)																
Spinograptus	*latespinosus*	Kozłowska-Dawidziuk 1997																
Doliograptus	*latus*	Lenz & Kozłowska-Dawidziuk 2002a																
Plectograptus	*macilentus*	(Törnquist 1887)																
Cometograptus	*marsupium*	(Lenz 1993b)																
Spinograptus	*munchi*	(Eisenack 1951)																
Gothograptus	*nassa*	(Holm 1890)		x	x		x											
Cometograptus	*nevadensis*	(Berry & Murphy 1975)																
Papiliograptus	*papilio*	Lenz & Kozłowska-Dawidziuk 2002a																
Papiliograptus?	*petilus*	Lenz & Kozłowska-Dawidziuk 2002a																
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)																
Spinograptus	*praerobustus*	Lenz & Kozłowska-Dawidziuk 2002a																
Spinograptus	*reticulolawsoni*	Kozłowska-Dawidziuk 1997																
Plectograptus	*robustus*	(Obut & Zaslavskaya 1983)																
Plectograptus	*wimani*	(Eisenack 1951)			cf													

praedeubeli-deubeli Zone retiolitids (continued)

Genus	Species	Author	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Baculograptus	*batesi*	Lenz & Kozłowska-Dawidziuk 2002a				x											
Baculograptus	*chainos*	(Lenz 1993b)				x											
Spinograptus	*clathrospinosus*	(Eisenack 1951)				x											
Retiolites (Gothograptus)	*gigantonassa*																
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)				cf											
Spinograptus	*latespinosus*	Kozłowska-Dawidziuk 1997				x											
Doliograptus	*latus*	Lenz & Kozłowska-Dawidziuk 2002a				x											
Plectograptus	*macilentus*	(Törnquist 1887)															
Cometograptus	*marsupium*	(Lenz 1993b)															
Spinograptus	*munchi*	(Eisenack 1951)															
Gothograptus	*nassa*	(Holm 1890)	x								x				x		
Cometograptus	*nevadensis*	(Berry & Murphy 1975)															
Papiliograptus	*papilio*	Lenz & Kozłowska-Dawidziuk 2002a				x											
Papiliograptus?	*petilus*	Lenz & Kozłowska-Dawidziuk 2002a				x											
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)															
Spinograptus	*praerobustus*	Lenz & Kozłowska-Dawidziuk 2002a				x											
Spinograptus	*reticulolawsoni*	Kozłowska-Dawidziuk 1997															
Plectograptus	*robustus*	(Obut & Zaslavskaya 1983)															
Plectograptus	*wimani*	(Eisenack 1951)															

ludensis Zone _s.s._ retiolitids

Genus	Species	Author	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Baculograptus	*chainos*	(Lenz 1993b)				x												
Spinograptus	*clathrospinosus*	(Eisenack 1951)				x												
Retiolites (Gothograptus)	*eximinassa*																	
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)																
Spinograptus	*latespinosus*	Kozłowska-Dawidziuk 1997																
Plectograptus	*macilentus*	(Törnquist 1887)				x												
Spinograptus	*munchi*	(Eisenack 1951)																
Gothograptus	*nassa*	(Holm 1890)																
Plectograptus?	*ovatus*	Kozłowska-Dawidziuk, Lenz & Štorch 2001																
Pseudoplectograptus	*praemacilentus*	Bouček & Münch 1952																
Spinograptus	*spinosus*	(Wood 1900)																
Plectograptus	*wimani*	(Eisenack 1951)																

***ludensis* Zone *s.s.* retiolitids (continued)**

Genus	**Species**	**Author**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**
Baculograptus	*chainos*	(Lenz 1993b)																
Spinograptus	*clathrospinosus*	(Eisenack 1951)											x					
Retiolites (Gothograptus)	*eximinassa*																	
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)																
Spinograptus	*latespinosus*	Kozłowska-Dawidziuk 1997																
Plectograptus	*macilentus*	(Törnquist 1887)																x
Spinograptus	*munchi*	(Eisenack 1951)																
Gothograptus	*nassa*	(Holm 1890)											x		x			
Plectograptus?	*ovatus*	Kozłowska-Dawidziuk, Lenz & Štorch 2001																x
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)													x			
Spinograptus	*spinosus*	(Wood 1900)																
Plectograptus	*wimani*	(Eisenack 1951)																

ludensis **Zone *s.s.* retiolitids (continued)**

Genus	Species	Author	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Baculograptus	*chainos*	(Lenz 1993b)																
Spinograptus	*clathrospinosus*	(Eisenack 1951)																
Retiolites (Gothograptus)	*eximinassa*				x													
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)																
Spinograptus	*latespinosus*	Kozłowska-Dawidziuk 1997																
Plectograptus	*macilentus*	(Törnquist 1887)			x													
Spinograptus	*munchi*	(Eisenack 1951)			x													
Gothograptus	*nassa*	(Holm 1890)			x													
Plectograptus?	*ovatus*	Kozłowska-Dawidziuk, Lenz & Štorch 2001																
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)																
Spinograptus	*spinosus*	(Wood 1900)																
Plectograptus	*wimani*	(Eisenack 1951)			cf													

ludensis Zone _s.s._ retiolitids (continued)

Genus	**Species**	**Author**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**
Baculograptus	*chainos*	(Lenz 1993b)				x											
Spinograptus	*clathrospinosus*	(Eisenack 1951)				x											
Retiolites (Gothograptus)	*eximinassa*																
"Spinograptus"	*karlsteinensis*	(Kozłowska-Dawidziuk, Lenz & Štorch 2001)				cf											
Spinograptus	*latespinosus*	Kozłowska-Dawidziuk 1997				x											
Plectograptus	*macilentus*	(Törnquist 1887)															
Spinograptus	*munchi*	(Eisenack 1951)															
Gothograptus	*nassa*	(Holm 1890)															
Plectograptus?	*ovatus*	Kozłowska-Dawidziuk, Lenz & Štorch 2001															
Pseudoplectograptus	*praemacilentus*	(Bouček & Münch 1952)															
Spinograptus	*spinosus*	(Wood 1900)				x											
Plectograptus	*wimani*	(Eisenack 1951)															

***lundgreni* Zone cyrtograptids**

Genus	**Species**	**Author**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Cyrtograptus	*carruthersi*	Lapworth 1876			x													
Cyrtograptus	*ellesae*	Gortani 1923																
Cyrtograptus	*gracilis*	Bouček 1931		cf				cf	cf									
Cyrtograptus	*hamatus*	(Baily 1861)		x	x		x	x	x	x		cf				x		
Cyrtograptus	*hemmanni*																	
Cyrtograptus	*lundgreni*	Tullberg 1883		x	x		x	x	x	x	x	x		x		x		
Cyrtograptus	*mancki*	Bouček 1931	cf									x						
Cyrtograptus	*multiramis*	Törnquist 1910		x					x									
Cyrtograptus	*perneri*	Bouček 1933		x					x									
Cyrtograptus	*pseudolundgreni*	Schauer 1972																
Cyrtograptus	*radians*	Törnquist 1887		x	x				x		x	x				x		
Cyrtograptus	*ramosus*	Bouček 1931																
Cyrtograptus	*trilleri*	Eisel 1914												x				
Cyrtograptus	*urbaneki*	Teller 1976																

lundgreni Zone cyrtograptids (continued)

Genus	**Species**	**Author**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**
Cyrtograptus	*carruthersi*	Lapworth 1876																
Cyrtograptus	*ellesae*	Gortani 1923		?														
Cyrtograptus	*gracilis*	Bouček 1931																
Cyrtograptus	*hamatus*	(Baily 1861)	x			x		?										
Cyrtograptus	*hemmanni*																	
Cyrtograptus	*lundgreni*	Tullberg 1883	x	x			cf	x			x				x	x		
Cyrtograptus	*mancki*	Bouček 1931																
Cyrtograptus	*multiramis*	Törnquist 1910																
Cyrtograptus	*perneri*	Bouček 1933																
Cyrtograptus	*pseudolundgreni*	Schauer 1972						x										
Cyrtograptus	*radians*	Törnquist 1887													x			
Cyrtograptus	*ramosus*	Bouček 1931																
Cyrtograptus	*trilleri*	Eisel 1914																
Cyrtograptus	*urbaneki*	Teller 1976																

lundgreni **Zone cyrtograptids (continued)**

Genus	**Species**	**Author**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**
Cyrtograptus	*carruthersi*	Lapworth 1876												x				
Cyrtograptus	*ellesae*	Gortani 1923											x	x	x			
Cyrtograptus	*gracilis*	Bouček 1931									cf							
Cyrtograptus	*hamatus*	(Baily 1861)	x		x	x		x		x	x		cf	x	x			
Cyrtograptus	*hemmanni*				x													
Cyrtograptus	*lundgreni*	Tullberg 1883	x	cf	x		?	x		x	x		x	x	x			x
Cyrtograptus	*mancki*	Bouček 1931								x	x							
Cyrtograptus	*multiramis*	Törnquist 1910																
Cyrtograptus	*perneri*	Bouček 1933					x	x		x	x		x		x			
Cyrtograptus	*pseudolundgreni*	Schauer 1972																
Cyrtograptus	*radians*	Törnquist 1887									x			x				
Cyrtograptus	*ramosus*	Bouček 1931											x					
Cyrtograptus	*trilleri*	Eisel 1914									x							
Cyrtograptus	*urbaneki*	Teller 1976						?					cf					

***lundgreni* Zone cyrtograptids (continued)**

Genus	**Species**	**Author**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**
Cyrtograptus	*carruthersi*	Lapworth 1876															
Cyrtograptus	*ellesae*	Gortani 1923															
Cyrtograptus	*gracilis*	Bouček 1931															
Cyrtograptus	*hamatus*	(Baily 1861)					x									x	
Cyrtograptus	*hemmanni*																
Cyrtograptus	*lundgreni*	Tullberg 1883	x	x	x		x	x		x	x		?			x	x
Cyrtograptus	*mancki*	Bouček 1931					x										
Cyrtograptus	*multiramis*	Törnquist 1910					x										
Cyrtograptus	*perneri*	Bouček 1933										x					
Cyrtograptus	*pseudolundgreni*	Schauer 1972															
Cyrtograptus	*radians*	Törnquist 1887					x					x					
Cyrtograptus	*ramosus*	Bouček 1931															
Cyrtograptus	*trilleri*	Eisel 1914											x				
Cyrtograptus	*urbaneki*	Teller 1976															

ludensis **Zone *s.l.* cyrtograptid**

Genus	Species	Author	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Cyrtograptus	*ellesae*	Gortani 1923		▨							▨			▨	▨			

Genus	Species	Author	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Cyrtograptus	*ellesae*	Gortani 1923		▨				ex gr cf			▨	▨						

Genus	Species	Author	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Cyrtograptus	*ellesae*	Gortani 1923	▨			▨		▨									▨	▨

Genus	Species	Author	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Cyrtograptus	*ellesae*	Gortani 1923							▨	▨		▨				▨	▨

lundgreni Zone monograptids A-O

Genus	Species	Author	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Euroclimacis	*adunca*	(Bouček 1931)		cf														
Monograptus	*ambiguus*	Jaeger 1991																
Monograptus?	*antennularius*	(Meneghini 1857)		x														
Monograptus?	*biglossa*	Lenz & Kozłowska-Dawidziuk 2001a		x														
Monograptus	*bogdanovi*	Obut & Sobolevskaya in Obut *et al.* 1967																
Monograptus	*boreus*	Obut & Sobolevskaya in Obut *et al.* 1967																
Colonograptus	*deubeli*	(Jaeger 1959)																
Pristiograptus	*dubius*	(Suess 1851)	x	x			x	x		ex gr		*s.l.*		x				
Monograptus	*firmus festinolatus*	Lenz & Melchin 1991						x										
Monograptus	*flemingii*	(Salter 1852)			x				x	x	x	x		x	x	x		
Monoclimacis	*flumendosae*	(Gortani 1922a)		x					x	x	cf	?				x		
Monoclimacis	*hemipristis*	(Meneghini 1857)																
Monograptus	*instrenuus*	Lenz & Melchin 1991		x			x	x							x			
Monograptus	*irfonensis*	Elles 1900																
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969																
Pristiograptus	*lodenicensis*	Přibyl 1943			x													
Pristiograptus	*meneghini*	(Gortani 1922a)																
Monograptus	*munchi*	Manck			x													
Monograptus	*mutuliferus longissimus*	Obut & Sobolevskaya in Obut *et al.* 1967																
Monograptus	*nganasanicus*	Obut & Sobolevskaya in Obut *et al.* 1965																
Monograptus	*opimus*	Lenz & Melchin 1991						x										
Monoclimacis	*oradovskayae*	Obut & Sobolevskaya in Obut *et al.* 1967																

***lundgreni* Zone monograptids A-O (continued)**

Genus	**Species**	**Author**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**
Euroclimacis	*adunca*	(Bouček 1931)																
Monograptus	*ambiguus*	Jaeger 1991																
Monograptus?	*antennularius*	(Meneghini 1857)																
Monograptus?	*biglossa*	Lenz & Kozłowska-Dawidziuk 2001a																
Monograptus	*bogdanovi*	Obut & Sobolevskaya in Obut *et al.* 1967																
Monograptus	*boreus*	Obut & Sobolevskaya in Obut *et al.* 1967																
Colonograptus	*deubeli*	(Jaeger 1959)																
Pristiograptus	*dubius*	(Suess 1851)	x	x		x	x	x							x	x		
Monograptus	*firmus festinolatus*	Lenz & Melchin 1991																
Monograptus	*flemingii*	(Salter 1852)	x	x		x	x	x				x			x	x		
Monoclimacis	*flumendosae*	(Gortani 1922a)						x							x			
Monoclimacis	*hemipristis*	(Meneghini 1857)																
Monograptus	*instrenuus*	Lenz & Melchin 1991						x										
Monograptus	*irfonensis*	Elles 1900																
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969						x										
Pristiograptus	*lodenicensis*	Přibyl 1943																
Pristiograptus	*meneghini*	(Gortani 1922a)		x														
Monograptus	*munchi*	Manck																
Monograptus	*mutuliferus longissimus*	Obut & Sobolevskaya in Obut *et al.* 1967																
Monograptus	*nganasanicus*	Obut & Sobolevskaya in Obut *et al.* 1965													x			
Monograptus	*opimus*	Lenz & Melchin 1991																
Monoclimacis	*oradovskayae*	Obut & Sobolevskaya in Obut *et al.* 1967																

lundgreni Zone monograptids A-O (continued)

Genus	Species	Author	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Euroclimacis	*adunca*	(Bouček 1931)																
Monograptus	*ambiguus*	Jaeger 1991			x													
Monograptus?	*antennularius*	(Meneghini 1857)																
Monograptus?	*biglossa*	Lenz & Kozłowska-Dawidziuk 2001a																
Monograptus	*bogdanovi*	Obut & Sobolevskaya in Obut *et al*. 1967																
Monograptus	*boreus*	Obut & Sobolevskaya in Obut *et al*. 1967																
Colonograptus	*deubeli*	(Jaeger 1959)													aff			
Pristiograptus	*dubius*	(Suess 1851)		*s.l.*	x		x			x	x		ex gr.	ex gr.	x	x	x	
Monograptus	*firmus festinolatus*	Lenz & Melchin 1991																
Monograptus	*flemingii*	(Salter 1852)	x	x	x	x	x	x		x	x			x	x	x	x	
Monoclimacis	*flumendosae*	(Gortani 1922a)								x	x		x	x	x		x	
Monoclimacis	*hemipristis*	(Meneghini 1857)								x								
Monograptus	*instrenuus*	Lenz & Melchin 1991																
Monograptus	*irfonensis*	Elles 1900						?										
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969																
Pristiograptus	*lodenicensis*	Přibyl 1943			x					x				x	x			
Pristiograptus	*meneghini*	(Gortani 1922a)						cf			x							
Monograptus	*munchi*	Manck												x				
Monograptus	*mutuliferus longissimus*	Obut & Sobolevskaya in Obut *et al*. 1967																
Monograptus	*nganasanicus*	Obut & Sobolevskaya in Obut *et al*. 1965																
Monograptus	*opimus*	Lenz & Melchin 1991																
Monoclimacis	*oradovskayae*	Obut & Sobolevskaya in Obut *et al*. 1967																

lundgreni Zone monographids A-O (continued)

Genus	Species	Author	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Euroclimacis	*adunca*	(Bouček 1931)					x										
Monograptus	*ambiguus*	Jaeger 1991															
Monograptus?	*antennularius*	(Meneghini 1857)															
Monograptus?	*biglossa*	Lenz & Kozłowska-Dawidziuk 2001a															
Monograptus	*bogdanovi*	Obut & Sobolevskaya in Obut *et al.* 1967								x							
Monograptus	*boreus*	Obut & Sobolevskaya in Obut *et al.* 1967								x							
Colonograptus	*deubeli*	(Jaeger 1959)															
Pristiograptus	*dubius*	(Suess 1851)	x	x	x						x		x		x	x	
Monograptus	*firmus festinolatus*	Lenz & Melchin 1991															
Monograptus	*flemingii*	(Salter 1852)	x	x	x		x	x		x	x	x	x		x	x	
Monoclimacis	*flumendosae*	(Gortani 1922a)		?	?			x				x	x				
Monoclimacis	*hemipristis*	(Meneghini 1857)	x														
Monograptus	*instrenuus*	Lenz & Melchin 1991															
Monograptus	*irfonensis*	Elles 1900															
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969															
Pristiograptus	*lodenicensis*	Přibyl 1943															
Pristiograptus	*meneghini*	(Gortani 1922a)															
Monograptus	*munchi*	Manck															
Monograptus	*mutuliferus longissimus*	Obut & Sobolevskaya in Obut *et al.* 1967								x							
Monograptus	*nganasanicus*	Obut & Sobolevskaya in Obut *et al.* 1965						x		x		x					
Monograptus	*opimus*	Lenz & Melchin 1991															
Monoclimacis	*oradovskayae*	Obut & Sobolevskaya in Obut *et al.* 1967								x							

lundgreni Zone monograptids P-Z

Genus	Species	Author	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Pristiograptus	*parvus*	Ulst 1974																
Pristiograptus	*praedubius*	Bouček 1931														cf		
Monograptus	*priodon*	(Bronn 1835)		x				x	x	x	x							
Monograptus	*proboscidatus*	Gortani 1922a							aff									
Pristiograptus	*pseudodubius*	(Bouček 1932)			x													
Mediograptus	*retroflexus*	Tullberg 1883														x		
Monograptus	*riccartonensis*	Lapworth 1876							aff		aff							
Pristiograptus	*sardous*	(Gortani 1922a)										x						
Monograptus	*shakhmardanicus*	Rinenberg 1965																
Monoclimacis	*simplex*	Lenz & Kozłowska-Dawidziuk 2001a		x														
Monograptus	*subflexilis*	Přibyl 1941																
Pristiograptus	*sumptuosus*	Přibyl 1941			x													
Testograptus	*testis*	(Barrande 1850)		x	x		x	x	x	x	x	x			x	x		
Monoclimacis	*vomerinus*	(Nicholson 1872)		cf										x				

***lundgreni* Zone monograptids P-Z (continued)**

Genus	Species	Author	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Pristiograptus	*parvus*	Ulst 1974						x		?								
Pristiograptus	*praedubius*	Bouček 1931																
Monograptus	*priodon*	(Bronn 1835)																
Monograptus	*proboscidatus*	Gortani 1922a																
Pristiograptus	*pseudodubius*	(Bouček 1932)	x															
Mediograptus	*retroflexus*	Tullberg 1883						aff										
Monograptus	*riccartonensis*	Lapworth 1876																
Pristiograptus	*sardous*	(Gortani 1922a)		x														
Monograptus	*shakhmardanicus*	Rinenberg 1965																
Monoclimacis	*simplex*	Lenz & Kozłowska-Dawidziuk 2001a																
Monograptus	*subflexilis*	Přibyl 1941																
Pristiograptus	*sumptuosus*	Přibyl 1941																
Testograptus	*testis*	(Barrande 1850)				x	x	x		x					x	x		
Monoclimacis	*vomerinus*	(Nicholson 1872)																

lundgreni Zone monograptids P-Z (continued)

Genus	Species	Author	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Pristiograptus	*parvus*	Ulst 1974																
Pristiograptus	*praedubius*	Bouček 1931																
Monograptus	*priodon*	(Bronn 1835)																
Monograptus	*proboscidatus*	Gortani 1922a																
Pristiograptus	*pseudodubius*	(Bouček 1932)	x					x			x			x	x		x	
Mediograptus	*retroflexus*	Tullberg 1883											ex. gr.					
Monograptus	*riccartonensis*	Lapworth 1876																
Pristiograptus	*sardous*	(Gortani 1922a)																
Monograptus	*shakhmardanicus*	Rinenberg 1965																
Monoclimacis	*simplex*	Lenz & Kozłowska-Dawidziuk 2001a																
Monograptus	*subflexilis*	Přibyl 1941								x	cf							
Pristiograptus	*sumptuosus*	Přibyl 1941												x				
Testograptus	*testis*	(Barrande 1850)	x	x	x		x			x	x			x				x
Monoclimacis	*vomerinus*	(Nicholson 1872)																

lundgreni Zone monograptids P-Z (continued)

Genus	Species	Author	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Pristiograptus	*parvus*	Ulst 1974															
Pristiograptus	*praedubius*	Bouček 1931															
Monograptus	*priodon*	(Bronn 1835)															
Monograptus	*proboscidatus*	Gortani 1922a								aff							
Pristiograptus	*pseudodubius*	(Bouček 1932)	x	x	cf			x					x				
Mediograptus	*retroflexus*	Tullberg 1883															
Monograptus	*riccartonensis*	Lapworth 1876															
Pristiograptus	*sardous*	(Gortani 1922a)															
Monograptus	*shakhmardanicus*	Rinenberg 1965										x					
Monoclimacis	*simplex*	Lenz & Kozłowska-Dawidziuk 2001a															
Monograptus	*subflexilis*	Přibyl 1941															
Pristiograptus	*sumptuosus*	Přibyl 1941															
Testograptus	*testis*	(Barrande 1850)	x				x	x	x	x	x	x				x	x
Monoclimacis	*vomerinus*	(Nicholson 1872)	ex. gr.														

parvus-nassa Zone monograptids

Genus	Species	Author	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Colonograptus	*deubeli*	(Jaeger 1959)																
Pristiograptus	*dubius*	(Suess 1851)				x										x		
Monograptus	*flemingii*	(Salter 1852)																
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969			x													
Pristiograptus	*lodenicensis*	Přibyl 1943			x													
Colonograptus	*ludensis*	(Murchison 1839)																
Pristiograptus	*ludlowensis*	(Bouček 1936)			x													
Pristiograptus	*parvus*	Ulst 1974			x													
Pristiograptus	*piltenensis*	Koren' & Ulst 1967			x													
Pristiograptus	*praedubius*	Bouček 1931														cf		
Pristiograptus	*pseudodubius*	(Bouček 1932)			x													
Lobograptus?	*sherrardae*	(Sherwin 1975)																
Pristiograptus	*virbalensis*	Paškevičius 1979																
Pristiograptus	*vulgaris*	Wood 1900																

parvus-nassa Zone monograptids (continued)

Genus	Species	Author	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Colonograptus	*deubeli*	(Jaeger 1959)																
Pristiograptus	*dubius*	(Suess 1851)	x			x									x	x		*s.l.*
Monograptus	*flemingii*	(Salter 1852)								x								
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969								aff								
Pristiograptus	*lodenicensis*	Přibyl 1943																
Colonograptus	*ludensis*	(Murchison 1839)								aff								
Pristiograptus	*ludlowensis*	(Bouček 1936)																
Pristiograptus	*parvus*	Ulst 1974				x												x
Pristiograptus	*piltenensis*	Koren' & Ulst 1967																
Pristiograptus	*praedubius*	Bouček 1931																
Pristiograptus	*pseudodubius*	(Bouček 1932)								cf								
Lobograptus?	*sherrardae*	(Sherwin 1975)																aff
Pristiograptus	*virbalensis*	Paškevičius 1979																
Pristiograptus	*vulgaris*	Wood 1900																

parvus-nassa Zone monograptids (continued)

Genus	Species	Author	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Colonograptus	*deubeli*	(Jaeger 1959)													aff			
Pristiograptus	*dubius*	(Suess 1851)		*s.l.*	x		x			x	x			ex. gr.	x	?		
Monograptus	*flemingii*	(Salter 1852)													x			
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969												x	x			
Pristiograptus	*lodenicensis*	Přibyl 1943												x				
Colonograptus	*ludensis*	(Murchison 1839)																
Pristiograptus	*ludlowensis*	(Bouček 1936)																
Pristiograptus	*parvus*	Ulst 1974		x	x						x			x				
Pristiograptus	*piltenensis*	Koren' & Ulst 1967												x				
Pristiograptus	*praedubius*	Bouček 1931																
Pristiograptus	*pseudodubius*	(Bouček 1932)												x	x			
Lobograptus?	*sherrardae*	(Sherwin 1975)																
Pristiograptus	*virbalensis*	Paškevičius 1979												x				
Pristiograptus	*vulgaris*	Wood 1900								x								

parvus-nassa Zone monograptids (continued)

Genus	Species	Author	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Colonograptus	*deubeli*	(Jaeger 1959)															
Pristiograptus	*dubius*	(Suess 1851)	x			x									x		
Monograptus	*flemingii*	(Salter 1852)															
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969				x											
Pristiograptus	*lodenicensis*	Přibyl 1943															
Colonograptus	*ludensis*	(Murchison 1839)															
Pristiograptus	*ludlowensis*	(Bouček 1936)															
Pristiograptus	*parvus*	Ulst 1974	x												cf		
Pristiograptus	*piltenensis*	Koren' & Ulst 1967															
Pristiograptus	*praedubius*	Bouček 1931															
Pristiograptus	*pseudodubius*	(Bouček 1932)															
Lobograptus?	*sherrardae*	(Sherwin 1975)															
Pristiograptus	*virbalensis*	Paškevičius 1979															
Pristiograptus	*vulgaris*	Wood 1900															

ludensis Zone *s.l.* monograptids A-R

Genus	Species	Author	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Lobograptus	*angustus*	Lenz 1995				x												
Monograptus	*auctus*	(Rickards 1965)			x													
Monograptus	*bohemicus*	(Barrande 1850)																
Lobograptus?	*claudiae*	Koren' 1992	x			x												
Lobograptus?	*cornuatus*	Lenz 1992				x												
Pristiograptus	*curtus*	(Elles & Wood 1911)			x													
Colonograptus	*deubeli*	(Jaeger 1959)			x	x												
Pristiograptus	*dubius*	(Suess 1851)	cf			x										x		x
Monograptus	*flemingii*	(Salter 1852)																
Colonograptus	*gerhardi*	(Kühne 1955)																
Pristiograptus	*gotlandicus*	(Perner 1899)																
Pristiograptus	*idoneus*	Koren' 1992																
Monograptus	*insperatus*	Koren' 1992																
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969	cf		x	x										x	x	x
Colonograptus	*ludensis*	(Murchison 1839)	cf		x	x							x			x	x	x
Pristiograptus	*ludlowensis*	(Bouček 1936)			x													
Monograptus	*moorsi*	Rickards & Wright 1997																
Pristiograptus	*parvus*	Ulst 1974																
Pristiograptus	*piltenensis*	Koren' & Ulst 1967			x													
Colonograptus	*praedeubeli*	Jaeger in Barca & Jaeger 1990				x												
Pristiograptus	*praedubius*	Bouček 1931														cf		
Monograptus	*priodon*	(Bronn 1835)	aff															
Pristiograptus	*pseudodubius*	(Bouček 1932)	cf															

ludensis Zone *s.l.* monograptids A-R (continued)

Genus	Species	Author	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Lobograptus	*angustus*	Lenz 1995																
Monograptus	*auctus*	(Rickards 1965)								cf								
Monograptus	*bohemicus*	(Barrande 1850)	cf															
Lobograptus?	*claudiae*	Koren' 1992													x	cf		
Lobograptus?	*cornuatus*	Lenz 1992																
Pristiograptus	*curtus*	(Elles & Wood 1911)																
Colonograptus	*deubeli*	(Jaeger 1959)					x	x		cf			x	x	x	x		x
Pristiograptus	*dubius*	(Suess 1851)	x		x			x	x	x			x	x	x	x		sl
Monograptus	*flemingii*	(Salter 1852)						x		?								
Colonograptus	*gerhardi*	(Kühne 1955)											?					x
Pristiograptus	*gotlandicus*	(Perner 1899)																
Pristiograptus	*idoneus*	Koren' 1992													x	x		
Monograptus	*insperatus*	Koren' 1992								x					x	x		
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969						x	x	x								
Colonograptus	*ludensis*	(Murchison 1839)	x		x			x	x	x			x	x	x	cf		x
Pristiograptus	*ludlowensis*	(Bouček 1936)																
Monograptus	*moorsi*	Rickards & Wright 1997							x									
Pristiograptus	*parvus*	Ulst 1974			?													
Pristiograptus	*piltenensis*	Koren' & Ulst 1967																
Colonograptus	*praedeubeli*	Jaeger in Barca & Jaeger 1990				x							x	x	x	x	x	x
Pristiograptus	*praedubius*	Bouček 1931																
Monograptus	*priodon*	(Bronn 1835)																
Pristiograptus	*pseudodubius*	(Bouček 1932)	x															

***ludensis* Zone *s.l.* monograptids A-R (continued)**

Genus	**Species**	**Author**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**
Lobograptus	*angustus*	Lenz 1995																
Monograptus	*auctus*	(Rickards 1965)			?										x			
Monograptus	*bohemicus*	(Barrande 1850)																
Lobograptus?	*claudiae*	Koren' 1992																
Lobograptus?	*cornuatus*	Lenz 1992																
Pristiograptus	*curtus*	(Elles & Wood 1911)												x				
Colonograptus	*deubeli*	(Jaeger 1959)		x	x		x		x					x		x		
Pristiograptus	*dubius*	(Suess 1851)		sl	x		sl			x			ex. gr.	ex. gr.	x	x		
Monograptus	*flemingii*	(Salter 1852)													x			
Colonograptus	*gerhardi*	(Kühne 1955)																
Pristiograptus	*gotlandicus*	(Perner 1899)								x								
Pristiograptus	*idoneus*	Koren' 1992																
Monograptus	*insperatus*	Koren' 1992																
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969												x	x	x		
Colonograptus	*ludensis*	(Murchison 1839)		x					x				x	ex. gr.	x	x		
Pristiograptus	*ludlowensis*	(Bouček 1936)												x				
Monograptus	*moorsi*	Rickards & Wright 1997																
Pristiograptus	*parvus*	Ulst 1974																
Pristiograptus	*piltenensis*	Koren' & Ulst 1967												x				
Colonograptus	*praedeubeli*	Jaeger in Barca & Jaeger 1990		x	x				x			x						
Pristiograptus	*praedubius*	Bouček 1931																
Monograptus	*priodon*	(Bronn 1835)																
Pristiograptus	*pseudodubius*	(Bouček 1932)													x			

***ludensis* Zone *s.l.* monograptids A-R (continued)**

Genus	**Species**	**Author**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**
Lobograptus	*angustus*	Lenz 1995				x											
Monograptus	*auctus*	(Rickards 1965)												x			
Monograptus	*bohemicus*	(Barrande 1850)															
Lobograptus?	*claudiae*	Koren' 1992				x					x						
Lobograptus?	*cornuatus*	Lenz 1992				x											
Pristiograptus	*curtus*	(Elles & Wood 1911)															
Colonograptus	*deubeli*	(Jaeger 1959)	x		cf	x											
Pristiograptus	*dubius*	(Suess 1851)	x	x		x					x		x		x		
Monograptus	*flemingii*	(Salter 1852)															
Colonograptus	*gerhardi*	(Kühne 1955)															
Pristiograptus	*gotlandicus*	(Perner 1899)															
Pristiograptus	*idoneus*	Koren' 1992									x						
Monograptus	*insperatus*	Koren' 1992									x						
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969				x											
Colonograptus	*ludensis*	(Murchison 1839)		x	x	x	x							x			
Pristiograptus	*ludlowensis*	(Bouček 1936)															
Monograptus	*moorsi*	Rickards & Wright 1997															
Pristiograptus	*parvus*	Ulst 1974			?												
Pristiograptus	*piltenensis*	Koren' & Ulst 1967															
Colonograptus	*praedeubeli*	Jaeger in Barca & Jaeger 1990	x			x					x				x		
Pristiograptus	*praedubius*	Bouček 1931															
Monograptus	*priodon*	(Bronn 1835)															
Pristiograptus	*pseudodubius*	(Bouček 1932)															

ludensis Zone *s.l.* monograptids S-Z

Genus	**Species**	**Author**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Colonograptus	*schedidoneus*	(Lenz 1994e)		▨		x					▨			▨	▨			
Lobograptus?	*sherrardae*	(Sherwin 1975)		▨		x					▨			▨	▨			
Testograptus	*testis*	(Barrande 1850)		▨							▨			▨	▨			
Monograptus	*uncinatus micropoma*	(Jaekel 1889)	cf	▨							▨			▨	▨			
Saetograptus	*varians*	Wood 1900		▨							▨			▨	▨			
Pristiograptus	*virbalensis*	Paškevičius 1979		▨							▨			▨	▨			
Pristiograptus	*vulgaris*	Wood 1900		▨							▨			▨	▨			

Genus	**Species**	**Author**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**
Colonograptus	*schedidoneus*	(Lenz 1994e)		▨							▨	▨						
Lobograptus?	*sherrardae*	(Sherwin 1975)		▨					x		▨	▨			x	x		
Testograptus	*testis*	(Barrande 1850)		▨				x		?	▨	▨						
Monograptus	*uncinatus micropoma*	(Jaekel 1889)		▨							▨	▨						
Saetograptus	*varians*	Wood 1900		▨						?	▨	▨						
Pristiograptus	*virbalensis*	Paškevičius 1979		▨							▨	▨						
Pristiograptus	*vulgaris*	Wood 1900		▨							▨	▨						

Genus	**Species**	**Author**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**
Colonograptus	*schedidoneus*	(Lenz 1994e)	▨			▨		▨	x								▨	▨
Lobograptus?	*sherrardae*	(Sherwin 1975)	▨			▨		▨									▨	▨
Testograptus	*testis*	(Barrande 1850)	▨			▨		▨									▨	▨
Monograptus	*uncinatus micropoma*	(Jaekel 1889)	▨			▨		▨									▨	▨
Saetograptus	*varians*	Wood 1900	▨			▨		▨									▨	▨
Pristiograptus	*virbalensis*	Paškevičius 1979	▨			▨		▨					x				▨	▨
Pristiograptus	*vulgaris*	Wood 1900	▨			▨		▨		x							▨	▨

***ludensis* Zone *s.l.* monograptids S-Z (continued)**

Genus	Species	Author	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Colonograptus	*schedidoneus*	(Lenz 1994e)				x											
Lobograptus?	*sherrardae*	(Sherwin 1975)				x					x						
Testograptus	*testis*	(Barrande 1850)															
Monograptus	*uncinatus micropoma*	(Jaekel 1889)															
Saetograptus	*varians*	Wood 1900															
Pristiograptus	*virbalensis*	Paškevičius 1979															
Pristiograptus	*vulgaris*	Wood 1900															

***praedeubeli-deubeli* Zone monograptids**

Genus	Species	Author	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Lobograptus	*angustus*	Lenz 1995				x												
Monograptus	*auctus*	(Rickards 1965)																
Lobograptus?	*claudiae*	Koren' 1992				x												
Lobograptus?	*cornuatus*	Lenz 1992				x												
Colonograptus	*deubeli*	(Jaeger 1959)				x												
Pristiograptus	*dubius*	(Suess 1851)				x												
Pristiograptus	*idoneus*	Koren' 1992																
Monograptus	*insperatus*	Koren' 1992																
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969																
Colonograptus	*ludensis*	(Murchison 1839)				x												
Monograptus	*moorsi*	Rickards & Wright 1997																
Colonograptus	*praedeubeli*	Jaeger in Barca & Jaeger 1990				x												
Colonograptus	*schedidoneus*	(Lenz 1994e)				x												
Lobograptus?	*sherrardae*	(Sherwin 1975)				x												

praedeubeli-deubeli Zone monograptids (continued)

Genus	Species	Author	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Lobograptus	*angustus*	Lenz 1995																
Monograptus	*auctus*	(Rickards 1965)																
Lobograptus?	*claudiae*	Koren' 1992													x	cf		
Lobograptus?	*cornuatus*	Lenz 1992																
Colonograptus	*deubeli*	(Jaeger 1959)													x	x		x
Pristiograptus	*dubius*	(Suess 1851)							x						x	x		sl
Pristiograptus	*idoneus*	Koren' 1992													x	x		
Monograptus	*insperatus*	Koren' 1992													x	x		
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969							x									
Colonograptus	*ludensis*	(Murchison 1839)							x									
Monograptus	*moorsi*	Rickards & Wright 1997							x									
Colonograptus	*praedeubeli*	Jaeger in Barca & Jaeger 1990				x							x		x	x		x
Colonograptus	*schedidoneus*	(Lenz 1994e)																
Lobograptus?	*sherrardae*	(Sherwin 1975)							x						x	x		

***praedeubeli-deubeli* Zone monograptids (continued)**

Genus	**Species**	**Author**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**
Lobograptus	*angustus*	Lenz 1995																
Monograptus	*auctus*	(Rickards 1965)			?													
Lobograptus?	*claudiae*	Koren' 1992																
Lobograptus?	*cornuatus*	Lenz 1992																
Colonograptus	*deubeli*	(Jaeger 1959)		x	x		x											
Pristiograptus	*dubius*	(Suess 1851)		sl	x		x											
Pristiograptus	*idoneus*	Koren' 1992																
Monograptus	*insperatus*	Koren' 1992																
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969																
Colonograptus	*ludensis*	(Murchison 1839)		x														
Monograptus	*moorsi*	Rickards & Wright 1997																
Colonograptus	*praedeubeli*	Jaeger in Barca & Jaeger 1990		x	x													
Colonograptus	*schedidoneus*	(Lenz 1994e)																
Lobograptus?	*sherrardae*	(Sherwin 1975)																

praedeubeli-deubeli Zone monograptids (continued)

Genus	Species	Author	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Lobograptus	*angustus*	Lenz 1995				x											
Monograptus	*auctus*	(Rickards 1965)															
Lobograptus?	*claudiae*	Koren' 1992				x					x						
Lobograptus?	*cornuatus*	Lenz 1992				x											
Colonograptus	*deubeli*	(Jaeger 1959)	x			x											
Pristiograptus	*dubius*	(Suess 1851)	x			x					x				x		
Pristiograptus	*idoneus*	Koren' 1992									x						
Monograptus	*insperatus*	Koren' 1992									x						
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969				x											
Colonograptus	*ludensis*	(Murchison 1839)															
Monograptus	*moorsi*	Rickards & Wright 1997															
Colonograptus	*praedeubeli*	Jaeger in Barca & Jaeger 1990	x			x					x				x		
Colonograptus	*schedidoneus*	(Lenz 1994e)				x											
Lobograptus?	*sherrardae*	(Sherwin 1975)				x					x						

ludensis Zone *s.s.* monograptids

Genus	Species	Author	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Monograptus	*auctus*	(Rickards 1965)																
Colonograptus	*deubeli*	(Jaeger 1959)																
Pristiograptus	*dubius*	(Suess 1851)				x												
Colonograptus	*gerhardi*	(Kühne 1955)																
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969				x												
Colonograptus	*ludensis*	(Murchison 1839)				x												
Colonograptus	*praedeubeli*	Jaeger in Barca & Jaeger 1990				x												
Colonograptus	*schedidoneus*	(Lenz 1994e)				x												
Lobograptus?	*sherrardae*	(Sherwin 1975)				x												

Genus	Species	Author	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Monograptus	*auctus*	(Rickards 1965)																
Colonograptus	*deubeli*	(Jaeger 1959)											x		x			
Pristiograptus	*dubius*	(Suess 1851)											x		x	x		sl
Colonograptus	*gerhardi*	(Kühne 1955)											?					x
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969																
Colonograptus	*ludensis*	(Murchison 1839)											x		x	cf		x
Colonograptus	*praedeubeli*	Jaeger in Barca & Jaeger 1990											x		x			x
Colonograptus	*schedidoneus*	(Lenz 1994e)																
Lobograptus?	*sherrardae*	(Sherwin 1975)																

ludensis **Zone *s.s.* monograptids (continued)**

Genus	Species	Author	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Monograptus	*auctus*	(Rickards 1965)			?													
Colonograptus	*deubeli*	(Jaeger 1959)			x													
Pristiograptus	*dubius*	(Suess 1851)		sl	x													
Colonograptus	*gerhardi*	(Kühne 1955)																
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969																
Colonograptus	*ludensis*	(Murchison 1839)		x														
Colonograptus	*praedeubeli*	Jaeger in Barca & Jaeger 1990			x													
Colonograptus	*schedidoneus*	(Lenz 1994e)																
Lobograptus?	*sherrardae*	(Sherwin 1975)																

Genus	Species	Author	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Monograptus	*auctus*	(Rickards 1965)															
Colonograptus	*deubeli*	(Jaeger 1959)				x											
Pristiograptus	*dubius*	(Suess 1851)				x											
Colonograptus	*gerhardi*	(Kühne 1955)															
Pristiograptus	*jaegeri*	Holland, Rickards & Warren 1969				x											
Colonograptus	*ludensis*	(Murchison 1839)				x											
Colonograptus	*praedeubeli*	Jaeger in Barca & Jaeger 1990				x											
Colonograptus	*schedidoneus*	(Lenz 1994e)				x											
Lobograptus?	*sherrardae*	(Sherwin 1975)				x											

Appendix 4 Occurrences of species in the three geographic regions

Lundgreni Zone neoglyptograptid species

Genus	Species	R1	R2	R3	Number of regions	Number of localities
Neoglyptograptus	*sussmilchi*			?	1	1

Ludensis Zone *s.l.* neoglyptograptid species

Genus	Species	R1	R2	R3	Number of regions	Number of localities
Neoglyptograptus	*sussmilchi*			z	1	1

Lundgreni Zone retiolitid species

Genus	Species	R1	R2	R3	Number of regions	Number of localities
Plectograptus	*absimilis*			z	1	1
Plectograptus	*aksuensis*			z	1	1
Cometograptus	*apoxys*	z			1	1
Cometograptus	*apsis*	z			1	1
Sagenograptus	*arctos*	z			1	1
Retiolites	*australis*	?			1	1
Cometograptus	*bicladis*	z			1	1
Spinograptus	*clathrospinosus*	z			1	1
Paraplectograptus	*eiseli*	z	z	z	3	8
Eisenackograptus	*eisenacki*	z		z	2	4
Paraplectograptus	*fidelis*			?	1	1
Cometograptus	*kirki*	z			1	1
Gothograptus	*kozlowskii*	z			1	1
Sokolovograptus	*lejskoviensis*		?	z	2	3
Cometograptus	*marsupium*	z			1	1
Paraplectograptus	*minutus*			z	1	1
Gothograptus	*nassa*	z	z	z	3	5
Cometograptus	*nevadensis*	z		z	2	3
Gothograptus	*obtectus*	z			1	1
Pseudoplectograptus	*praemacilentus*	z	z	z	3	8
Gothograptus	*pseudospinosus*	z	z	z	3	5
Pseudoplectograptus	*sagenus*	z			1	2
Pseudoplectograptus	*simplex*	z			1	2
Gothograptus	*tenuis*	z		z	2	2
Sokolovograptus	*textor*	z		z	2	3

parvus-nassa Zone retiolitids

Genus	Species	R1	R2	R3	Number of regions	Number of localities
Spinograptus	*clathrospinosus*		z		1	1
Plectograptus	*dubius*	aff?			1	1
Retiolites (Gothograptus)	*gigantonassa*		z		1	1
Gothograptus	*intermedius*	z			1	1
"Spinograptus"	*karlsteinensis*		z		1	1
Sokolovograptus	*lejskoviensis*	z			1	1
Gothograptus	*nassa*	z	z	z	3	13
Cometograptus	*nevadensis*		cf		1	1
Pseudoplectograptus	*praemacilentus*	z		z	2	2
Gothograptus	*pseudospinosus*	z			1	1
Spinograptus	*reticulolawsoni*		?		1	1
Spinograptus	*spinosus*	z			1	1

Ludensis Zone *s.l.* retiolitid species

Genus	Species	R1	R2	R3	Number of regions	Number of localities
Baculograptus	*batesi*	z			1	1
Baculograptus	*chainos*	z		z	2	2
Spinograptus	*clathrospinosus*	z	z	z	3	7
Retiolites (Gothograptus)	*eximinassa*		z		1	1
Retiolites (Gothograptus)	*gigantonassa*		z		1	1
"Spinograptus"	*karlsteinensis*	cf	z		2	2
Spinograptus	*latespinosus*	z			1	2
Doliograptus	*latus*	z			1	1
Spinograptus	*lawsoni*	z			1	2
Plectograptus	*macilentus*	z	z	z	3	5
Cometograptus	*marsupium*			z	1	1
Spinograptus	*munchi*	z	z	z	3	4
Gothograptus	*nassa*	z	z	z	3	14
Cometograptus	*nevadensis*	z			1	2
Plectograptus?	*ovatus*		z		1	1
Papiliograptus	*papilio*	z			1	1
Papiliograptus?	*petilus*	z			1	1
Pseudoplectograptus	*praemacilentus*			z	1	2
Spinograptus	*praerobustus*	z			1	1
Gothograptus	*pseudospinosus*			z	1	1
Spinograptus	*reticulolawsoni*	z			1	1
Plectograptus	*robustus*	z		z	2	3
Spinograptus	*spinosus*	z			1	2
Sokolovograptus	*textor*			z	1	1
Agastograptus	*wimani*	z	cf		2	3

praedeubeli-deubeli **Zone retiolitids**

Genus	**Species**	**R1**	**R2**	**R3**	**Number of regions**	**Number of localities**
Baculograptus	*batesi*	z			1	1
Baculograptus	*chainos*	z		z	2	2
Spinograptus	*clathrospinosus*	z	z		2	3
Retiolites (Gothograptus)	*gigantonassa*		z		1	1
"Spinograptus"	*karlsteinensis*	cf	z		2	2
Spinograptus	*latespinosus*	z			1	2
Doliograptus	*latus*	z			1	1
Plectograptus	*macilentus*	z			1	1
Cometograptus	*marsupium*			z	1	1
Spinograptus	*munchi*		z		1	1
Gothograptus	*nassa*	z	z	z	3	6
Cometograptus	*nevadensis*	z			1	1
Papiliograptus	*papilio*	z			1	1
Papiliograptus?	*petilus*	z			1	1
Pseudoplectograptus	*praemacilentus*			z	1	1
Spinograptus	*praerobustus*	z			1	1
Spinograptus	*reticulolawsoni*	z			1	1
Plectograptus	*robustus*	z		z	2	2
Agastograptus	*wimani*	?	cf		2	2

ludensis **Zone *s.s.* retiolitids**

Genus	**Species**	**R1**	**R2**	**R3**	**Number of regions**	**Number of localities**
Baculograptus	*chainos*	z			1	1
Spinograptus	*clathrospinosus*	z		z	2	2
Retiolites (Gothograptus)	*eximinassa*		z		1	1
"Spinograptus"	*karlsteinensis*	cf			1	1
Spinograptus	*latespinosus*	z			1	1
Plectograptus	*macilentus*	z	z		2	3
Spinograptus	*munchi*		z		1	1
Gothograptus	*nassa*		z	z	2	3
Plectograptus?	*ovatus*		z		1	1
Pseudoplectograptus	*praemacilentus*			z	1	1
Spinograptus	*spinosus*	z			1	1
Agastograptus	*wimani*		cf		1	1

***Lundgreni* Zone cyrtograptids**

Genus	**Species**	**R1**	**R2**	**R3**	**Number of regions**	**Number of localities**
Cyrtograptus	*carruthersi*	z			1	1
Cyrtograptus	*ellesae*	z	?		2	3
Cyrtograptus	*gracilis*	cf	cf		2	2
Cyrtograptus	*hamatus*	z	z	?	3	13
Cyrtograptus	*hemmanni*		z		1	1
Cyrtograptus	*lundgreni*	z	z	z	3	23
Cyrtograptus	*mancki*	z	z		2	5
Cyrtograptus	*multiramis*	z	z		2	2
Cyrtograptus	*perneri*	z	z	z	3	7
Cyrtograptus	*pseudolundgreni*			z	1	1
Cyrtograptus	*radians*	z	z	z	3	7
Cyrtograptus	*ramosus*	z			1	1
Cyrtograptus	*trilleri*	z	z		2	3
Cyrtograptus	*urbaneki*	? cf			1	2

***Ludensis* Zone *s.l.* cyrtograptid**

Genus	**Species**	**R1**	**R2**	**R3**	**Number of regions**	**Number of localities**
Cyrtograptus	*ellesae*		ex gr cf		1	1

Lundgreni Zone monograptids

Genus	Species	R1	R2	R3	Number of regions	Number of localities
Euroclimacis	*adunca*	cf	z		2	2
Monograptus	*ambiguus*		z		1	1
Monograptus?	*antennularius*	z			1	1
Monograptus?	*biglossa*	z			1	1
Monograptus	*bogdanovi*			z	1	1
Monograptus	*boreus*			z	1	1
Colonograptus	*deubeli*	aff			1	1
Pristiograptus	*dubius*	z	z	z	3	18
Monograptus	*firmus festinolatus*	z			1	1
Monograptus	*flemingii*	z	z	z	3	24
Monoclimacis	*flumendosae*	z	z	z	3	12
Monoclimacis	*hemipristis*	z	z		2	2
Monograptus	*instrenuus*	z		z	2	3
Monograptus	*irfonensis*	?			1	1
Pristiograptus	*jaegeri*			z	1	1
Pristiograptus	*lodenicensis*	z	z		2	4
Pristiograptus	*meneghini*	cf	z		2	3
Monograptus	*munchi*	z			1	1
Monograptus	*mutuliferus longissimus*			z	1	1
Monograptus	*nganasanicus*			z	1	3
Monograptus	*opimus*	z			1	1
Monoclimacis	*oradovskayae*			z	1	1
Pristiograptus	*parvus*			z	1	2
Pristiograptus	*praedubius*	cf			1	1
Monograptus	*priodon*	z			1	2
Monograptus	*proboscidatus*	aff		aff	2	2
Pristiograptus	*pseudodubius*	z	z	z	3	9
Mediograptus	*retroflexus*	z		aff	2	3
Monograptus	*riccartonensis*	aff			1	2
Pristiograptus	*sarduous*	z	z		2	2
Monograptus	*shakhmardanicus*			z	1	1
Monoclimacis	*simplex*	z			1	1
Monograptus	*subflexilis*	z	cf		2	2
Pristiograptus	*sumptuousus*	z			1	1
Testograptus	*testis*	z	z	z	3	19
Monoclimacis	*vomerinus*	z	ex gr		2	2

parvus-nassa Zone monograptids

Genus	Species	R1	R2	R3	Number of regions	Number of localities
Colonograptus	*deubeli*	aff			1	1
Pristiograptus	*dubius*	z	z	z	3	11
Monograptus	*flemingii*	z		z	2	2
Pristiograptus	*jaegeri*	z		aff	2	4
Pristiograptus	*lodenicensis*	z			1	1
Colonograptus	*ludensis*			aff	1	1
Pristiograptus	*ludlowensis*	z			1	1
Pristiograptus	*parvus*	z	z		2	7
Pristiograptus	*piltenensis*	z			1	1
Pristiograptus	*praedubius*	cf			1	1
Pristiograptus	*pseudodubius*	z		cf	2	3
Lobograptus?	*sherrardae*		aff		1	1
Pristiograptus	*virbalensis*	z			1	1
Pristiograptus	*vulgaris*	z			1	1

Ludensis Zone *s.l.* monograptids

Genus	Species	R1	R2	R3	Number of regions	Number of localities
Lobograptus	*angustus*	z			1	1
Monograptus	*auctus*	z	?	cf	3	5
Monograptus	*bohemicus*		cf		1	1
Lobograptus?	*claudiae*	z		z	2	3
Lobograptus?	*cornuatus*	z			1	1
Pristiograptus	*curtus*	z			1	1
Colonograptus	*deubeli*	z	z	z	3	15
Pristiograptus	*dubius*	z	z	z	3	18
Monograptus	*flemingii*	z		z	2	3
Colonograptus	*gerhardi*		z	?	2	2
Pristiograptus	*gotlandicus*	z			1	1
Pristiograptus	*idoneus*			z	1	1
Monograptus	*insperatus*			z	1	2
Pristiograptus	*jaegeri*	z	z	z	3	8
Colonograptus	*ludensis*	z	z	z	3	19
Pristiograptus	*ludlowensis*	z			1	1
Monograptus	*moorsi*			z	1	1
Pristiograptus	*parvus*	?	?		2	2
Pristiograptus	*piltenensis*	z			1	1
Colonograptus	*praedeubeli*	z	z	z	3	13
Pristiograptus	*praedubius*	cf			1	1
Monograptus	*priodon*	aff			1	1
Pristiograptus	*pseudodubius*	z	z		2	3
Colonograptus	*schedidoneus*	z		z	2	2
Lobograptus?	*sherrardae*	z		z	2	3
Testograptus	*testis*			z	1	2
Monograptus	*uncinatus micropoma*	cf			1	1
Saetograptus	*varians*			?	1	1
Pristiograptus	*virbalensis*	z			1	1
Pristiograptus	*vulgaris*	z			1	1

praedeubeli-deubeli Zone monograptids

Genus	Species	R1	R2	R3	Number of regions	Number of localities
Lobograptus	*angustus*	z			1	1
Monograptus	*auctus*		?		1	1
Lobograptus?	*claudiae*	z		z	2	2
Lobograptus?	*cornuatus*	z			1	1
Colonograptus	*deubeli*	z	z	z	3	6
Pristiograptus	*dubius*	z	z	z	3	18
Pristiograptus	*idoneus*			z	1	1
Monograptus	*insperatus*			z	1	1
Pristiograptus	*jaegeri*	z		z	2	2
Colonograptus	*ludensis*	z	z	z	3	3
Monograptus	*moorsi*			z	1	1
Colonograptus	*praedeubeli*	z	z	z	3	9
Colonograptus	*schedidoneus*	z			1	1
Lobograptus?	*sherrardae*	z		z	2	3

ludensis Zone *s.s.* monograptids

Genus	Species	R1	R2	R3	Number of regions	Number of localities
Monograptus	*auctus*		z		1	1
Colonograptus	*deubeli*	z	z	z	3	4
Pristiograptus	*dubius*	z	z	z	3	6
Colonograptus	*gerhardi*		z	?	2	2
Pristiograptus	*jaegeri*	z			1	1
Colonograptus	*ludensis*	z	z	z	3	5
Colonograptus	*praedeubeli*	z	z	z	3	5
Colonograptus	*schedidoneus*	z			1	1
Lobograptus?	*sherrardae*	z			1	1