

High palaeolatitude (Hodh, Mauritania) recovery of graptolite faunas after the Hirnantian (end Ordovician) extinction event

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Abstract

Marine shales directly overlying lower Hirnantian (uppermost Ordovician) glacially related sediments in Mauritania (North-West Africa) have produced a rich graptolite fauna spanning the Ordovician-Silurian boundary in an area of high palaeolatitude. The lowermost transgressive sandy shales are barren of graptolites, but overlying shales show a sudden appearance of a diverse fauna indicative of the terminal Ordovician *persculptus* Zone, suggesting that with improving conditions, colonisation by a relatively cold-tolerant fauna was possible. This fauna is replaced by a low diversity assemblage dominated by long ranging taxa, probably representing the basal Silurian *acuminatus* and *atavus* Zones. With the extinction of the *persculptus* Zone fauna, conditions were still hostile to warm water Silurian graptolites, and a *Normalograptus* fauna was again established. A sudden influx of fairly diverse taxa marks the base of the *acinaces* Zone and the establishment of a typical Lower Silurian fauna with the establishment of warmer water conditions.

Keywords: glaciation, graptolites, Ordovician, radiation, Silurian, West Africa.

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1. Introduction.

The uppermost Ordovician Hirnantian Stage saw a short-lived but extensive glaciation over large portions of Gondwana. This was associated with changes in sea-level and oceanic geochemistry, and had a profound effect on global palaeoenvironments (e.g. Brenchley 1984, 1988; Brenchley *et al.* 1994, Underwood *et al.* 1997). These changes resulted in many groups of organisms undergoing severe reductions in diversity or rapid taxonomic turnover (e.g. Brenchley 1984). The net effect of this is recognised as one of the largest Phanerozoic extinction events (Raup and Sepkoski 1982), particularly at lower taxonomic levels.

Upper Ordovician sediments from Gondwana provide extensive direct evidence of glaciation, with glacial diamictites and associated glaciofluvial and

glaciomarine sediments being recorded in northern Africa (e.g. Beuf *et al.* 1971; Deynoux 1980), Arabia (Vaslet, 1990), South Africa (e.g. Rust 1981) and South America (e.g. Sanchez *et al.* 1991). These indicate an extensive ice cap centred over central Africa, which at the time lay over the South Pole (Scotese and McKerrow 1990). Although the base of the glacial sediments is generally erosional (e.g. Beuf *et al.* 1971; Deynoux 1980), the timing of the initiation of the glaciation is directly known in Morocco (Destombes *et al.* 1985) and in Algeria (Paris *et al.* 1995), whilst graptolites indicative of the Rawtheyan are known from Niger (Legrand 1993). Dropstone horizons at lower palaeolatitudes are seen associated with, or immediately underlying, a Hirnantian fauna (e.g. Storch 1990). The glacial sediments are overlain by strongly transgressive sediments of late Hirnantian age, containing either a shelly *Hirnantia* fauna (Legrand 1988) or a *persculptus* Zone graptolite fauna (Willefert 1988; McClure 1988, Rickards *et al.* 1996).

At lower palaeolatitudes this glacial event was manifested by a range of palaeoenvironmental changes. A major regression is seen in shelf sequences, whilst basinal sequences provide evidence for oxygenation of the sea floor (e.g. Brenchley 1988). In some cases, the changes are associated with horizons containing dropstones (e.g. Storch 1990). There is also stable isotope evidence for a cooling of ocean water (e.g. Brenchley *et al.* 1994; Marshall *et al.* 1997) and a disruption of the oceanic carbon cycle (e.g. Underwood *et al.* 1997). The upper part of the Hirnantian is represented by strongly transgressive sequences with extensive deposition of organic rich shales containing a *persculptus* Zone graptolite fauna within both shelf and basinal settings. This transgression generally continued into the Early Silurian.

It is within these lower palaeolatitude sites that the faunal succession has been most extensively studied. The base of the Hirnantian is marked by an extinction event effecting many groups of organisms (e.g. Sepkoski 1995), with diverse assemblages being replaced by eurytopic or generalistic faunas such as the *Hirnantia* fauna (Brenchley 1988). This event severely reduced planktic graptolite diversity, with the sudden disappearance of diverse Ashgill faunas dominated by members of the Dicranograptidae, Diplograptidae and Orthograptidae (the DDO fauna of Melchin and Mitchell 1991). Only the genera *Normalograptus* and *Persculptograptus* (*sensu* Koren' and Rickards 1996) are known to have passed through the Hirnantian (Melchin and Mitchell 1991), although some late Hirnantian graptolites may represent "Lazarus" genera. Within the later part of the Hirnantian (*persculptus* Zone of authors) and earliest Silurian, the transgression is associated with a diversification of graptolitic faunas, probably associated with the extinction of many elements of the eurytopic *Hirnantia* fauna (Brenchley 1988). The graptolite diversification is well recorded from a number of low palaeolatitude sites (e.g. Williams 1986; Melchin and Mitchell 1991), and consisted of a radiation within the genus *Normalograptus*, resulting in the appearance of several new genera, including the appearance of uniserial and dimorphograptid taxa near the base of the Silurian.

The post-extinction recovery of shelly faunas was slow, with stable brachiopod communities not re-established until late in the Llandovery (Harper and Rong 1995). Graptolite communities appear to have recovered more rapidly, with progressive and rapid radiation through the Ordovician-Silurian boundary interval. By the mid Llandovery, high diversity faunas including a wide variety of morphotypes had become established (e.g. Rickards *et al.* 1977). Graptolite faunas from this post-extinction interval are known from a number of high palaeolatitude sites in Northwest Africa (e.g. Legrand, 1970, 1986, 1988; Deynoux 1980; Destombes and Willefert 1988; Willefert 1988). Comparisons of the nature of the post-extinction recovery between these sites with better documented faunas from

Europe, North America and Asia has, however, been hindered by the endemic nature of some of the species (Legrand 1986) and inaccessibility of many of the sites (Deynoux 1980). As the Hirnantian extinction event was triggered by high palaeolatitude glaciogenic environmental change, study of graptolite faunas at high palaeolatitude sites would be expected to provide direct evidence of the factors controlling the post-extinction recovery.

2. Geological setting

The Hodh area of Mauritania contains extensive exposures of undeformed sediments of dominantly end Proterozoic to Early Devonian age (Fig.1)(see Deynoux *et al.*, 1985 for a review). The Upper Ordovician of this area represents one of the best documented examples of glacially related sediments deposited during the Hirnantian glacial event (Deynoux 1980, Deynoux 1985). The glacial sediments rest on a marked erosion surface with associated glacial pavements and glaciotectionic features. The sediments are dominated by complex suites of glaciofluvial deposits with locally preserved patches of glaciogenic diamictite at the base. These are overlain in turn by glaciomarine diamictites passing upward into dropstone-bearing muddy sandstones and shales. The remainder of the succession consists dominantly of shales deposited in an open marine outer shelf setting. This marine succession is interrupted by three laterally extensive sandstone beds, 1 to 10 m thick, which serve as useful marker beds and have been numbered as R1, R2 and R3 (Deynoux 1980)(Fig.2).

The transgressive glaciomarine and marine sediments overlie older glacial sediments with an onlapping relationship. The oldest transgressive sediments are present only in the Nseirat area (section 77, Fig. 2), above marker bed R1. The lower part of these transgressive shales contain thin lenses of coarse grained muddy sandstones bearing exotic striated dropstones. The muddy sandstones disappear rapidly upward, 5 metres below the lowest graptolite bearing shale horizon (Deynoux, 1980). The shales are capped by marker bed R2, which consists of a ferruginous and muddy fine-grained sandstone with intense bioturbation and scattered ferruginous and phosphatic ooids. Continued onlapping of marine shales onto glaciofluvial sandstones above R2 is seen at the westernmost site at El Boueti (section 60, Fig. 2). Marker bed R2 is overlain by monotonous shales only interrupted by few thin ferruginous sandy horizons including the thicker and most extensive marker bed R3.

3. Material and methods

Graptolites and other associated fossils were collected from seven sites located over about 120 km of outcrop, corresponding to sections described by Deynoux (1980) (Fig.2). The stratigraphic position of all specimens was recorded relative to the main sandstone marker horizons (R1 to R3). As the general lithostratigraphic succession at all sites was similar, graphic correlation techniques were used to compile a composite graptolite succession, with all samples being projected onto the most complete measured section at Nseirat (section 77; Fig. 3).

The quality of preservation of the graptolites is variable, dependant on both the primary diagenesis and subsequent tropical weathering effects. Most of the graptolites were preserved as flattened organic films, which varied from fairly pristine periderm to highly weathered vague remnants. Occasional specimens were preserved in relief by a steinkern of a white mineral, possibly gypsum replacing

weathered pyrite. Most graptolites were studied under water or alcohol with a binocular microscope, although some of the shale samples were friable enough to disintegrate under liquid (this resulted in the loss of two of the specimens figured). Although the study focuses on graptolites, associated biotas of conularids, brachiopods, chitinozoans and rare trilobites are present and are currently under study.

4. Faunas and Biostratigraphy

Analysis of the graptolite faunas collected revealed over 20 species. The majority of these are taxa of wide or global distribution, with endemic African forms being probably limited to a single rare species. The cosmopolitan nature of the faunas allows direct comparison with European assemblage biozones (*sensu* Rickards 1995), without the necessity of constructing a local zonal scheme (as in Legrand 1986).

The lowermost 15 meters of the transgressive shales appear to be barren of graptolites. These probably represent sediments deposited, at least in the basal part, under glaciomarine conditions, as striated dropstones are present near the base. About five metres below the top of this lowermost shale unit, there is a sudden appearance of a fauna with graptolites being common and often well preserved. The fauna is fairly diverse, consisting of about eight species. It is dominated by *Persculptograptus persculptus* s.l. (Elles and Wood), with collections including both wide and narrow individuals. Although some studies have separated wide and narrow forms as *P. persculptus* s.s. and '*P. parvulus* (Lapworth) respectively (e.g. Zalasiewicz and Tunnicliff 1994), this was not considered practical here as both morphologies appeared to form end members within a variable population. Wide and narrow specimens of *Normalograptus cf. extraordinarius* (Sobolevskaya) are also common at some levels. Associated with these species are rarer specimens of *Normalograptus ex gr. normalis* (Lapworth), *N. pseudovenustus* (Legrand), '*Glyptograptus*' aff. *avitus* Davies and two species of *Sudburigraptus*. This fauna is typical of the terminal Ordovician *persculptus* Zone, with most of the species present appearing to have a near global distribution. *N. extraordinarius* is usually considered an Upper Rawtheyan to Lower Hirnantian (*extrordinarius* Zone) form (e.g. Williams 1983), however the record of *Normalograptus cf. extraordinarius* in post-glacial sediments associated with a typical *persculptus* Zone fauna suggests that *Normalograptus cf. extraordinarius* survived into the *persculptus* Zone.

The shales forming a middle interval above the first sandstone marker bed R2 of Deynoux (1980) are more extensively exposed, and were sampled at several different localities. At the sites where samples were collected from immediately above this marker bed to about 10 metres above, a very similar fauna to that lower down was recovered. The dominant graptolites are again *P. persculptus* s.l., here dominated by populations of only small individuals, larger specimens being recorded in only two collections. This species is associated with *N. ex gr. normalis*, which becomes increasingly common up section. Some collections contain abundant specimens of *N. pseudovenustus*, whilst the last specimens of '*G.*' aff. *avitus* and *Sudburigraptus* were encountered about five metres above R2. Rare specimens of *Normalograptus ?mirneyensis* (Obut and Sobolevskaya) and *N. miserabilis* (Elles and Wood) were also recorded. A single sample yielded specimens of *Glyptograptus* aff. *lacinosus* Churkin and Carter about seven metres above R2, just before the lowest occurrence of *Normalograptus transgradiens* (Wærn).

This fauna is generally biostratigraphically undiagnostic, and contains elements of both the *persculptus* Zone and basal Silurian *acuminatus* Zone.

Persculptograptus persculptus s.l., especially small forms such as *P. parvulus*, continues well into the *acuminatus* Zone (e.g. Zalasiewicz and Tunnicliff 1994). *Normalograptus pseudovenustus* has not been recorded in the *acuminatus* Zone, whilst *Glyptograptus avitus* has only been recorded as extending into its basal part (Williams 1986), but neither species have been widely recognised within Ordovician-Silurian boundary sections. *Glyptograptus lacinosus*, however, has only been recognised within the *acuminatus* Zone (Churkin and Carter 1970), as has *Normalograptus transgradiens* (Wærn 1948). It is therefore likely that the base of the Silurian occurs somewhere within this interval, probably within the upper part. In the absence of *Parakidograptus acuminatus* (Nicholson), which defines the base of the Silurian, the exact position of the base will remain conjectural.

The upper half of this middle shale interval, up to sandstone marker bed R3, contains an even less diagnostic, and often poorly preserved, fauna. The vast majority of graptolites recovered from this interval are specimens of the long ranging and cosmopolitan species *N. ex gr. normalis*. The lower half of the interval contains occasional specimens of *N. transgradiens*, an unidentified *Normalograptus* and rare specimens of *Paraclimacograptus innotatus innotatus* (Nicholson). The upper part contains rare *Pseudorthograptus ?obuti* (Rickards and Koren') and specimens of *Normalograptus medius* (Törnquist) and *N. rectangularis* (M'Coy).

This is the highest interval seen to show an onlapping relationship. Faunas collected from the onlapping beds just below sandstone R3 at section 60 contain only *Normalograptus ex gr. normalis*.

This interval contains very few graptolites of biostratigraphic use. *P. innotatus innotatus* and *N. rectangularis* are widespread forms within the *acuminatus* Zone. *P. obuti* is not recorded prior to the *cyphus* Zone, although other closely related forms appear in the *atavus* Zone (Koren' and Rickards 1996). It is therefore probable that this interval includes the upper part of the *acuminatus* Zone and the *atavus* Zone.

The shales above bed R3 were sampled at three localities which yielded similar faunas. The graptolite fauna is dominated by specimens of *Neodiplograptus modestus modestus* (Lapworth), with the subspecies *N. modestus tenuis* (Rickards) also being present in one sample. Less common are specimens of *Lagarograptus acinaces* (Törnquist), *Metaclimacograptus hughesi* (Nicholson) and *Glyptograptus sp.*, with *Normalograptus imperfectus* (Legrand) present immediately above bed R3. The long ranging *N. ex gr. normalis*, *N. medius* and *N. rectangularis* are also all present but generally uncommon.

This fauna is typical of the *acinaces* Zone and, with the exception of the African endemic *Normalograptus imperfectus*, is similar to *acinaces* Zone faunas worldwide.

5. Comparison with other sites

The general stratigraphy of the Mauritanian sections is rather similar to that of many of the graptolitic Ordovician-Silurian boundary sequences worldwide (see Cocks and Rickards 1988 for a review). The *extraordinarius* Zone of the Hirnantian is marked by either strongly regressive facies, glaciogenic sediments or an increase in sediment oxygenation (Brenchley 1988). This is usually followed in the *persculptus* Zone by strongly transgressive, and commonly euxinic, facies. These transgressive graptolitic shales commonly persist through much of the Rhuddanian. The Ordovician-Silurian boundary is defined on the first appearance of the graptolite *Parakidograptus acuminatus* at the section at Dob's Linn, Scotland, and by correlation, elsewhere. Neither this species or the co-occurring *Akidograptus*

ascensus Davies were seen in the Mauritanian samples, despite their otherwise wide distribution (although Willefert 1988 records fragments of ?*Akidograptus*). It is possible that the absence of *Parakidograptus* and *Akidograptus* is due, at least in part, to their preference for deeper water environments (S. H. Williams *pers. comm.*). The *persculptus* Zone is marked in most sections by a rapid increase in graptolite diversity marking a major evolutionary radiation event. This radiation continues within the earliest Silurian with the appearance of new genera. This continued radiation is not seen in the Mauritanian material, where the diversity decreases with the extinction of the *persculptus* Zone forms. A typical Early Silurian fauna only becomes established in the *acinaces* Zone.

The graptolite species consist primarily of taxa known almost worldwide, and are similar to faunas recorded previously in North Africa in Morocco (Destombes and Willefert 1988). This contrasts with contemporary graptolite faunas from Algeria, which consist of relatively low diversity faunas of largely endemic species not recorded elsewhere (Legrand 1970, 1986). High palaeolatitude faunas from Argentina (Rickards *et al.* 1996) contain both widely distributed taxa and '*Climacograptus*' *innotatus brasiliensis* Ruedemann, a taxon that appears to be endemic to South America.

6. Faunal events

The distributions of graptolite taxa (see Fig. 4) clearly show a succession of distinct faunal events between the first occurrence of graptolites in the post-glacial environment and the establishment of a diverse typical Llandovery fauna. This faunal change is not necessarily coincident with either local or global eustatic changes in sealevel, or with standard biozonal boundaries.

The first recognised occurrence of graptolites within the section is not far above the last well documented dropstones of glaciomarine origin and is marked by the establishment of a diverse upper Hirnantian assemblage. The subsequent disappearance of *Normalograptus* cf. *extraordinarius* (event 2) coincides with a shallowing event. This relative change in water depth is probably due to local parasequence progradation within an overall transgressive system. Other elements of the fauna appear unaffected by these changes in water depth. The somewhat later loss of the remaining members of this Late Hirnantian fauna (event 3) allows the re-establishment of *Normalograptus* ex gr. *normalis* dominated assemblages throughout the remainder of the second progradational parasequence. Several species of post-extinction taxa are also present, but are numerically insignificant. The transgressive shales above the sandstone marker bed R3 contain a distinctly different fauna from that below (event 4). This fauna is relatively high diversity and is dominated by species belonging to several post-extinction genera including *Neodiplograptus*, *Lagarograptus*, *Metaclimacograptus* and *Glyptograptus* ss.

7. Interpretation of faunal changes

The sudden appearance of a diverse *persculptus* Zone fauna presumably marks an increased suitability of ocean water conditions for graptolites allowing the establishment of a complex planktic ecosystem. *Normalograptus* and *Persculptograptus* are genera already present below the base of the Hirnantian, although *Normalograptus pseudovenustus* appears to represent a species which has originated after the extinction event. The origins of the *avitus* group of '*Glyptograptus*' and *Sudburigraptus* are obscure, (Koren' and Rickards 1996), but

they may well be from ancestors with a pattern H or I proximal development (of Mitchell 1987), as yet unrecognised amongst the small Late Ordovician 'orthograptids'. The presence of numerous specimens of *Normalograptus* cf. *extraordinarius* within an otherwise typical *persculptus* Zone fauna, is unusual, but has been recorded elsewhere (e.g. Yolkin *et. al.* 1988), and may suggest that this species persisted rather later at higher palaeolatitudes.

Normalograptus cf. *extraordinarius* disappears before the rest of its contemporaries, at a sandstone coincident with a shallowing episode. It is unlikely that the last appearance of this species is directly related to this change in sea-level, as the co-occurring fauna persists. It is more likely that this point marks the final extinction of this species in the lower part of the *persculptus* Zone.

Other members of the *persculptus* Zone fauna persist above the sandstone marker bed into the next transgressive sequence. Here they co-occur with *Glyptograptus* aff. *lacinosus*, a 'true' *Glyptograptus*, probably of the *tamariscus* group. This may mark the first appearance of a genus (or species group) which originated after the extinction event.

The sudden replacement of this fauna by a low diversity, *Normalograptus* ex gr. *normalis* dominated assemblage is a feature not recorded at other Ordovician-Silurian boundary sites. The basal Silurian is marked at sites of mid to low palaeolatitude by a replacement of the *persculptus* Zone fauna by new taxa, generally associated with a rapid diversity increase (e.g. Rickards 1988). The sparse biostratigraphic evidence available suggests that the *persculptus* Zone fauna progressively died out during the early part of the *acuminatus* Zone, much as is seen elsewhere. The lack of replacement of this upper Hirnantian fauna by new taxa within their high palaeolatitude environment suggests that the conditions that were hospitable for the *persculptus* Zone graptolites were unsuitable for their usual ecological replacement species. *N. ex gr. normalis* is almost ubiquitous within Ashgill to mid Llandovery graptolite-bearing sediments. It is therefore likely to have been a true generalist, able to tolerate a wide range of environmental conditions, including some hostile to the bulk of other graptolites. There are several factors which may have limited graptolite diversity, the most likely being connection to the ocean, water temperature (e.g. Berry and Wilde 1990), water depth and available nutrient. Uncommon occurrences of other characteristic Silurian species suggest that a connection with open marine conditions existed, whilst there is no sedimentological evidence for the impoverished fauna being due to a sudden decrease in water depth. The large numbers of graptolites suggests that nutrients were, at least periodically, abundant and were not a limiting factor. It is therefore probable that the controlling factor was water temperature. The species typical of the Hirnantian had either survived a major glaciation event, or evolved during it or within its immediate aftermath. Hirnantian graptolites had therefore evolved to be tolerant of a range of conditions, including cold waters. By the earliest Silurian, the re-establishment of pre-glaciation conditions allowed warm, stratified oceans to exist in all but the highest palaeolatitudes. During this period, the evolution of the new graptolite taxa has been well recorded from localities in Europe and Asia which lay within the palaeoequatorial zone (Scotese and McKerrow 1990). It is therefore unlikely that any of the newly evolved forms were as well adapted for life in cold water as the generalist *Normalograptus* ex gr. *normalis*.

It is only during the subsequent sea-level rise that the typical lower Silurian fauna became established. The incoming of typical *acinaces* Zone faunas was associated with the first appearance of taxa which generally appear at lower horizons. *Neodiplograptus modestus* is not seen below this level, which it dominates, but is

well known from the *persculptus* and *acuminatus* Zones in Europe and China (e.g. Rickards 1995). It is therefore likely that environmental constraints prevented this Silurian fauna from appearing earlier. The appearance of this new fauna during a transgression, suggests that the transgression brought low latitude type watermasses over North Africa for the first time.

8. Discussion

The effects of the Hirnantian extinction event was particularly pronounced amongst the graptolites (e.g. Sepkoski 1995; Melchin and Mitchell 1986). Despite this, the recovery of graptolite faunas through the late Hirnantian and Llandovery was more rapid than that of other fossil groups (Sepkoski 1995; Kaljo 1996) and involved the origination of a range of novel rhabdosome forms (Rickards *et al.* 1977).

Graptolite assemblages from the *extraordinarius* Zone, coeval with the Hirnantian glacial maximum, are known at far fewer sites worldwide than graptolite faunas from immediately underlying and overlying zones. This is due both to the common occurrence of erosion surfaces at this level producing erosional gaps within many sections and the change to facies unsuitable for graptolite preservation. Known faunas are of low diversity and consist largely of species of very wide geographic distribution. The species recorded fall into two general categories. Species such as *N. ex gr. normalis* and *N. miserabilis* first appear long before the extinction event and continue long after. They represent ecological generalist species, able to survive in rapidly changing conditions and environments hostile to other graptolites. Other species, notably *Normalograptus extraordinarius* and *Persculptograptus persculptus*, first appear within the *pacificus* Subzone immediately before the extinction event and die out during the initial recovery interval. These species therefore show preadaptation to surviving the extinction event, but were possibly out-competed during the initial recovery period when more specialist taxa started to fill available niches. The recorded occurrence of most *extraordinarius* Zone taxa in pre-extinction faunas (e.g. Williams 1986) suggests that there were few appearances of new forms during the height of the extinction event.

Assemblages from the *persculptus* Zone, which includes the initial post-glacial transgression, are known from many sites. These faunas are generally of higher diversity than those of the *extraordinarius* Zone, and include many new taxa. The sudden appearance of these new species indicates a very rapid period of speciation, and it is probable that most of the Llandovery graptolite clades originated within this period. This radiation continued into the earliest Silurian with the continued appearance of new genera (Melchin and Mitchell 1991), but it is probable that only a single additional clade, that including *Pseudorthograptus* and the retiolitids, appeared during this time (Koren' and Rickards 1996).

The graptolite faunas within the *persculptus* Zone and immediately above may be divided into a number of guilds of survivor and recovery taxa, although these are not generally easily compared with those recognised amongst other taxa at other extinction events (e.g. Kauffman and Harries 1996, Harries *et. al.* 1996). The long ranging *N. ex gr. normalis* and *N. miserabilis* are true ecological generalists being present in a range of palaeoenvironments over a long time span. They are also highly opportunistic, with occasional superabundant 'flood' occurrences, generally in the absence of other taxa. Within the Mauritanian sequence, such a flood occurrence is seen within the basal Silurian, with similar occurrences recorded at other levels elsewhere. *N. extraordinarius* and *P. persculptus* constitute survivor species ranging up into the recovery period. Of these species, *N. extraordinarius* appears less well

adapted to coexist with the new taxa. The only record of this species from the *persculptus* Zone is in Mauritania, and even then does it not survive to the Ordovician-Silurian boundary. The greater geographic and stratigraphic range of *P. persculptus* in the recovery interval suggests that it was more of an ecological generalist, able to coexist with a range of other graptolites.

The base of the *persculptus* Zone at most sites sees the appearance of many new species. The origination of some post-extinction taxa is well known. *Atavograptus ceryx* (Hutt and Rickards), and hence all subsequent monograptids, is considered to have originated from a narrow 'diplograptid' probably referable to *Persculptograptus* or *Normalograptus* (Hutt and Rickards 1970), and many of the Llandovery 'diplograptid' genera originated from *Normalograptus* (Koren' and Rickards 1996). Although the origins of other taxa are more obscure, there is no evidence to suggest that they arose from progenitor species that evolved within the extinction event, a mechanism suggested by Kauffman and Harries (1996) to be a dominant feature of recovery faunas. Many of the new species that appear within the *persculptus* Zone are largely or entirely restricted to it. These forms, such as *Normalograptus pseudovenustus* and *Glyptograptus avitus*, are wide ranging and commonly very abundant, and may be recognised as representing a distinct evolutionary guild within the recovery fauna. Immediately on evolving, these taxa opportunistically filled a relatively short-lived niche, and are as such probably best termed evolutionary opportunists.

The *persculptus* Zone faunas of Mauritania are dominated by species within these three evolutionary guilds:- opportunistic generalists, survivor taxa and recovery opportunists. At lower palaeolatitude sites elsewhere, *persculptus* Zone taxa are accompanied by the first appearance of species that were either long ranging or initiated a long ranging lineage. The general absence of the forms within the Mauritanian *persculptus* Zone, and their rarity in overlying basal Silurian sediments suggests that in contrast to the evolutionary opportunist taxa, the lineages were initially largely restricted to low palaeolatitudes. This more restricted initial range but greater longevity of these 'Silurian' lineages suggest that they evolved as more specialist taxa within the diverse niches made available by the development of a warm, stratified ocean.

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Appendix: Taxonomic notes

Normalograptus ex gr. normalis (Lapworth). (Fig. 5; A, B, C.). The numerous specimens assigned to this species fall within the morphological range usually attributed to it. The wide range of morphology has led some authors (e.g. Legrand 1986) to assign specimens to a range of subspecies. It is here considered that within the material studied the range of shape is continuous between these 'subspecies' and as such any attempt of this subdivision is arbitrary. It is possible, however, that morphometric study of large, well preserved populations could lead to the separation of a number of discrete morphological forms allowing a subdivision of this species. The material of this taxon contains a number of synrhabdosomes.

Normalograptus sp. ? *normalis* (Lapworth) (Fig. 5; D.). This single specimen is similar to *Normalograptus normalis* in its general morphology, but differs in having very rapid proximal widening giving an overall fusiform morphology. The affinities are uncertain, but it may be an extreme morphology of *Normalograptus ex gr. normalis*.

Normalograptus cf. extraordinarius (Sobolevskaya). (Fig. 5; G, H, I.). This species, probably recorded as 'a new amplexograptid form' by Willefert (1988), is similar to specimens of *Normalograptus extraordinarius* recorded elsewhere. There is considerable variation within the population, with occasional very narrow specimens as well as the typical wide, fusiform rhabdosomes. This is similar to the variation recorded in material from Siberia (Koren' *et al.* 1983). The Mauritanian material in general appears to possess a somewhat longer theca 1^1 with a less well developed notch at its junction with the sicula than material recorded from elsewhere. It is not here, however, considered that these variations represent significant differences from the type material of *Normalograptus extraordinarius*, but it may in future be shown that *Normalograptus extraordinarius* s.l. represents several distinct varieties or subspecies.

Normalograptus pseudovenustus (Legrand). (Fig. 5; L, M.). A number of specimens referred to this species were recorded. First described as '*Climacograptus venustus*' Legrand, this species was renamed due to the name being preoccupied (Legrand 1986), but with minimal figures and no redescription. Examples of this species are rather variable in form, and have previously been split between several subspecies and forms (Legrand 1986), a scheme which was not considered appropriate here. The majority of specimens have a prominent virgella, as is seen in most of the type assemblage, but specimens with a small virgella, as dominate in the population from Dob's Linn (Williams 1983), were also recorded.

Persculptograptus persculptus s.l. (Elles and Wood). (Fig. 5; S, T, U, V, W.). It has long been recognised that the specimens referred to '*Glyptograptus persculptus*' form a very variable group (e.g. Davies 1929), which has recently been shown to include '*Diplograptus bohemicus*' Marek (Storch and Loydell 1996). '*Glyptograptus persculptus*' has recently been assigned as the type species of the genus *Persculptograptus* (Koren' and Rickards 1996). As *Persculptograptus persculptus*, along with several other species, appears to possess a well defined morphology easily separable from *Normalograptus*, the name is retained here despite some doubt as to whether a separate generic name is justified (S. H. Williams *pers. comm.*). Within the species' type area in Wales, it is generally considered that two species are present (Zalasiewicz and Tunnicliff 1994)- the older and larger *Persculptograptus persculptus* and the smaller and later *Persculptograptus parvulus* (Lapworth). Within the Mauritanian material, however, this division is not as clear. Most of the populations collected contain specimens of a range of sizes, with maximum widths

and thecal spacings varying between those typical of the two species. It was noticed, however, that although smaller specimens were present in almost all samples, larger individuals (maximum width over 1.8 mm) were not always present, being dominant within the lower samples, but only present in a small number of collections higher up section. For this reason, it was chosen not to split *Persculptograptus persculptus* s.l. into separate species, but to indicate which populations contained larger individuals. Several synrhabdosomes were recorded.

Glyptograptus aff. *avitus* Davies. (Fig. 5; Y, Z.). Small and commonly poorly preserved specimens agree well with descriptions of *Glyptograptus avitus* from Scotland, but differ in lacking the bifurcating virgella characteristic of this species. This difference, however, could be preservational.

Sudburigraptus spp. (Fig. 5; AA, BB.). Two species of this poorly known genus (erected to include many small Llandovery '*Orthograptus*' species by Koren' and Rickards (1996)) were recorded, with no well preserved specimens. *Sudburigraptus* sp. II may be co-specific with '*Orthograptus truncatus abbreviatus*' Elles and Wood of Hutt 1975.

Pseudorthograptus (*Pseudorthograptus*) ?*obuti* (Rickards and Koren'). (Fig. 5; HH). Two specimens are referred to this species, although the diagnostic spinose structures are not seen, probably due to the quality of preservation. *Pseudorthograptus* (*Pseudorthograptus*) *obuti* has not previously been recorded prior to the *cyphus* Zone.

Neodiplograptus modestus (Lapworth). (Fig. 5; CC, DD, EE.). Numerous specimens assigned to this species were recorded from the upper parts of the sections. They are rather variable, but compare well to specimens recorded from elsewhere. At a similar horizon in Algeria specimens referred to various subspecies of '*Diplograptus*' *africanus* Legrand have been recorded (Legrand 1970, 1986). These differ from the Mauritanian species in having a greater maximum width and poorly developed proximal genicular spines. It is possible, however, that these represent large specimens of a variable species, as '*Diplograptus*' *africanus posterior* Legrand appears to be indistinguishable from *Neodiplograptus modestus modestus*. One sample contained very narrow specimens referred to *Neodiplograptus modestus tenuis* (Rickards)(Fig. 5; FF.).

Captions to Figures

Fig. 1

Locality map of the Hodh area, showing positions of the sections studied (from Deynoux 1980).

Fig. 2

Lithostratigraphic correlation of the sections described in Deynoux (1980).

Fig. 3

Composite graptolite range chart for the Ordovician-Silurian boundary interval, Hodh, Mauritania, showing probable biostratigraphy.

All samples projected on to log of Nseirat section by graphic correlation.

Fig. 4

Comparison of evidence for local sea-level changes and relative abundances of the groups of graptolites, demonstrating the main faunal events.

Event 1 marks the initial colonisation by graptolites, event 2 marks the appearance of a diverse late Hirnantian fauna, event 3 marks the disappearance of *N. cf. extraordinarius* coinciding with a hiatus, event 4 marks the replacement of the late Hirnantian fauna by a low diversity *Normalograptus* fauna and event 5 marks the incoming of a diverse early Silurian fauna coinciding with a flooding event.

Note that the evidence for relative sea-level changes is taken largely from regional facies and onlap relationships.

Fig. 5

Camera Lucida drawings of representative graptolites from the Ordovician-Silurian boundary interval, Hodh, Mauritania. All specimens are in Liverpool City Museum and Art Gallery (prefix LIVCM), except specimens E and II which completely exfoliated during figuring.

A (1997.108.A), B(1997.108.B), C (1997.108.C). *Normalograptus* ex gr. *normalis* (Lapworth). Representative specimens showing variation. D (1997.108.D). *Normalograptus* sp. ? *normalis* (Lapworth). E, F (1997.108.E). *Normalograptus miserabilis* (Elles and Wood). G (1997.108.F), H (1997.108.G). *Normalograptus* cf. *extraordinarius* (Sobolevskaya). Typical forms. I (1997.108.H). *Normalograptus* cf. *extraordinarius* (Sobolevskaya). Narrow form. J (1997.108.J). *Normalograptus medius*. K (1997.108.K). *Normalograptus rectangularis*. L (1997.108.L), M (1997.108.M). *Normalograptus pseudovenustus* (Legrand). Specimens with prominent virgella. N (1997.108.N), O (1997.108.P). *Normalograptus* aff. *rectangularis* (M'Coy). P (1997.108.Q). *Normalograptus ?mirneyensis* (Obut & Sobolevskaya). Q (1997.108.R), R (1997.108.S). *Normalograptus imperfectus* (Legrand). Proximal and distal fragments. S (1997.108.T), T (1997.108.U), U (1997.108.V), V (1997.108.W), W (1997.108.X). *Persculptograptus persculptus* s.l. (Elles and Wood). Note wide variation in maximum width and thecal spacing. X (1997.108.Y). *Metaclimacograptus hughesi* (Nicholson). Y (1997.108.Z), Z (1997.108.AA). *Glyptograptus* aff. *avitus* Davies. AA (1997.108.AB). *Sudburigraptus* sp I. BB (1997.108.AC). *Sudburigraptus* sp II. CC (1997.108.AD), DD (1997.108.AE), EE (1997.108.AF). *Neodiplograptus modestus modestus* (Lapworth). FF (1997.108.AG). *Neodiplograptus modestus tenuis* (Rickards). GG (1997.108.AH). *Glyptograptus lacinosus* Churkin and Carter. HH (1997.108.AJ). *Pseudorthograptus (Pseudorthograptus) ?obuti* (Rickards and Koren'). II. *Paraclimacograptus innotatus innotatus* (Nicholson). JJ (1997.108.AK), KK (1997.108.AL), LL (1997.108.AM), MM (1997.108.AN). *Lagarograptus acinaces* (Törnquist). Distal, proximal and median fragments.

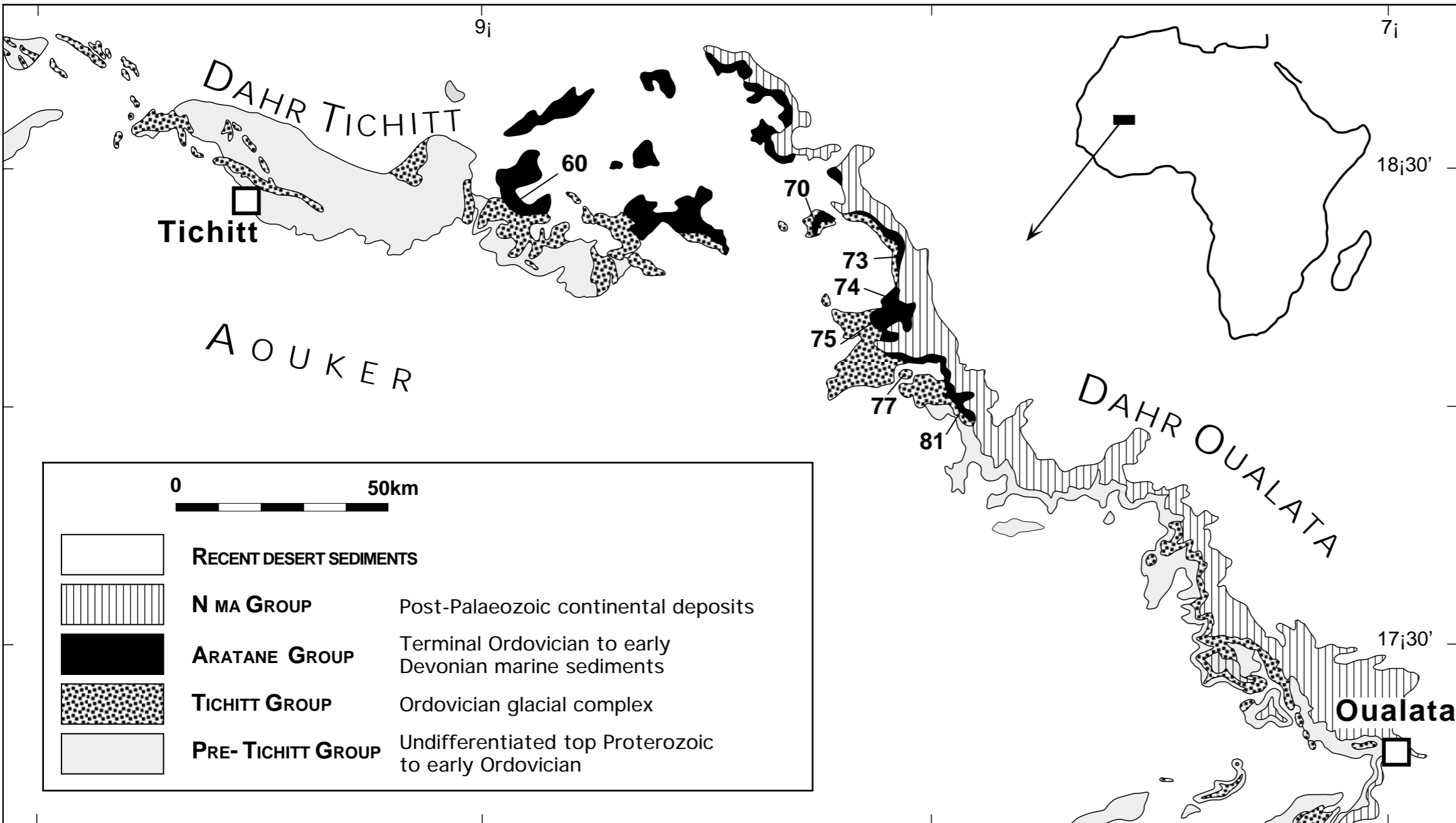


Figure 1. Locality map of the Hodh area, showing positions of the sections studied (from Deynoux 1980).

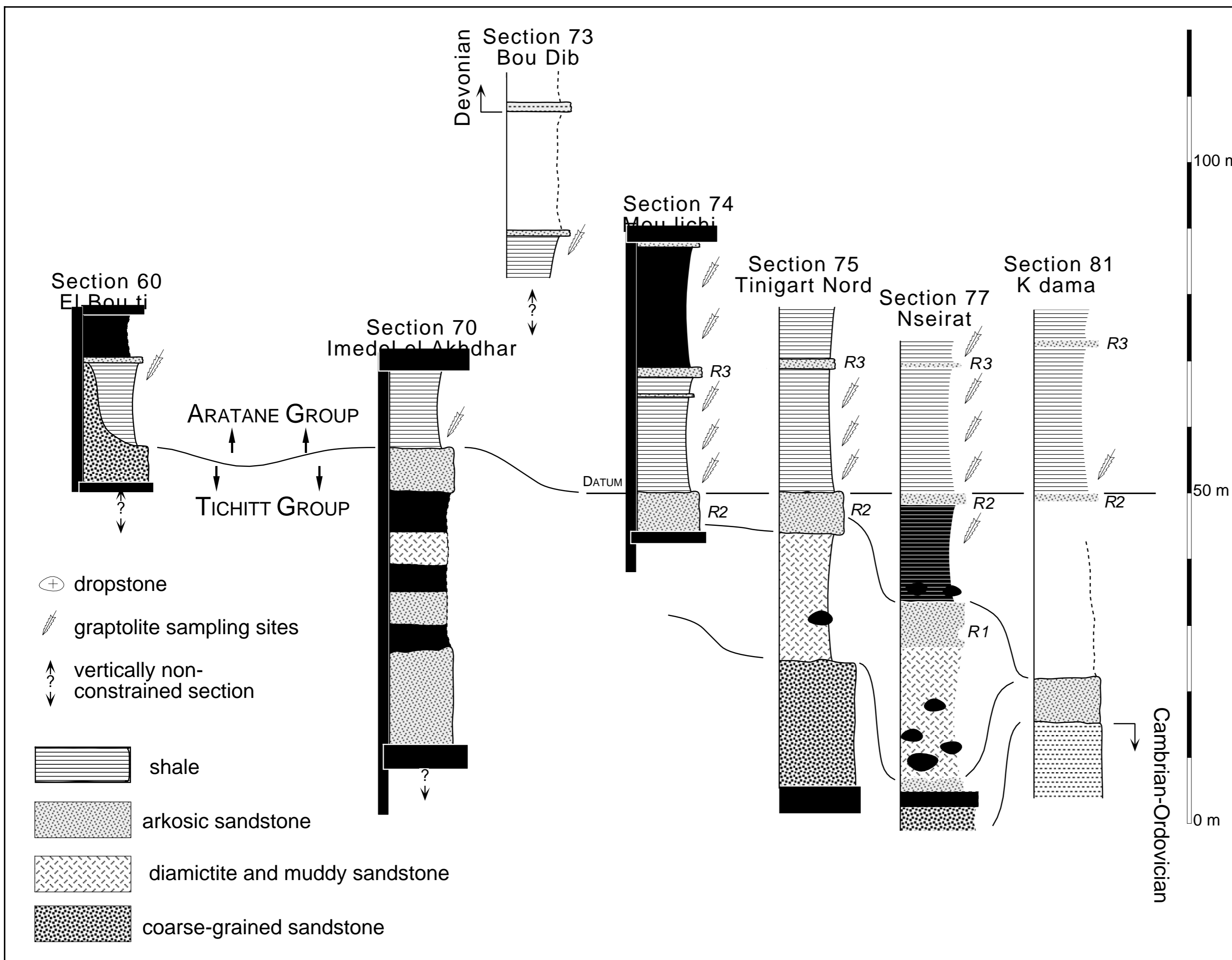


Figure 2. Lithostratigraphic correlation of the sections described in Deynoux (1980).

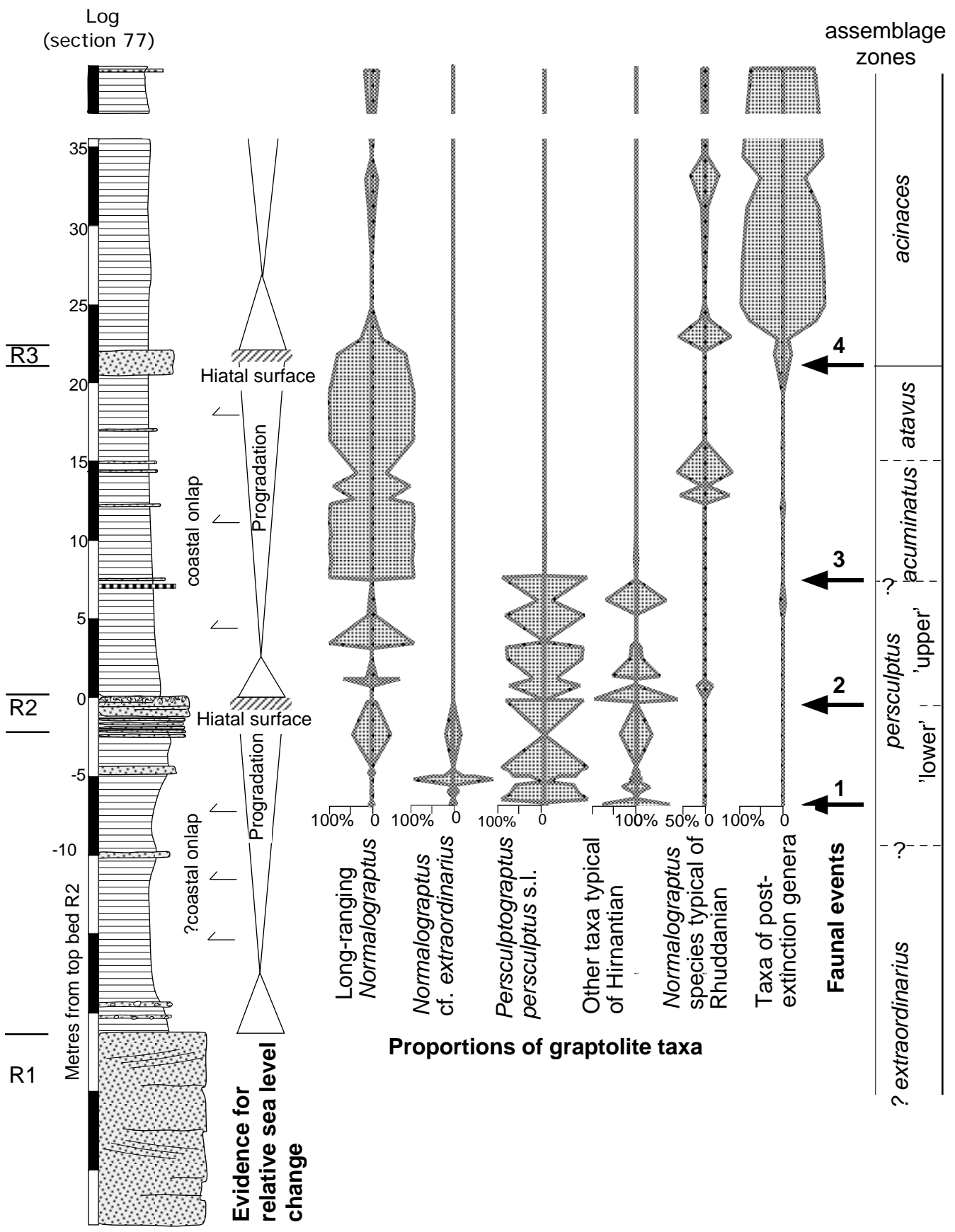


Figure 4.

