

Environment preference of eurypterids – indications for freshwater adaptation?

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Abstract. Publications on Palaeozoic eurypterids have been analyzed in sight of paleology, biotope preference of this animals and supposed evolutionary pathways from marine to freshwater environments. The outcome is, that during the Late Palaeozoic these arthropods adapted increasingly to near-shore shallow marine and obviously to freshwater biotopes as well. Interestingly, all known freshwater occurrences are restricted to the paralic foredeeps of the Hercynian orogen. Only one exception has been found in the Late Carboniferous (Westphalian D) of the intramontane Saar basin. Therefore, question rises on the nature of this basin in Late Westphalian time.

Introduction

Eurypterids are a class of Arthropods with a range from the Ordovician to Permian and a maximum distribution during the Silurian and Devonian. All pre-Devonian eurypterids are found in marine deposits, but some Devonian and later groups are believed to have inhabited freshwater environments (Donovan 2001). The goal of this study was, to analyze the literature for hard facts on facies pattern and biotope preference of Late Palaeozoic eurypterids. The main question was, if any real proof for freshwater adaptation exists.

Systematic of Eurypterids

Eurypterids are a subclass of Merostomata which belong to the Chelicerata (see Fig. 1) which again belong to the Arthropoda.

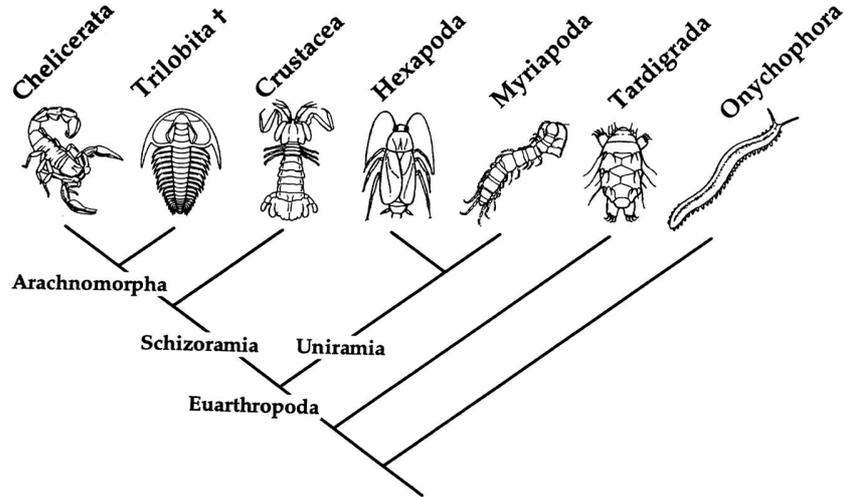


Fig.1. Relationships between extant and fossil classes of arthropods. (Singer ed. 1999)

Morphology of Eurypterids

The body of *Eurypterus* (Fig. 2) as a typical member of the Eurypterids is divided into three parts, the prosoma, the mesosoma and the metasoma. At first the prosoma is composed commonly of the first six segments with its paired appendages and is protected by a carapace with dorsal eyes and a mouth at the ventral side. The mesosoma has seven segments with gill and genital function. The metasoma consists of further segments and the telson.

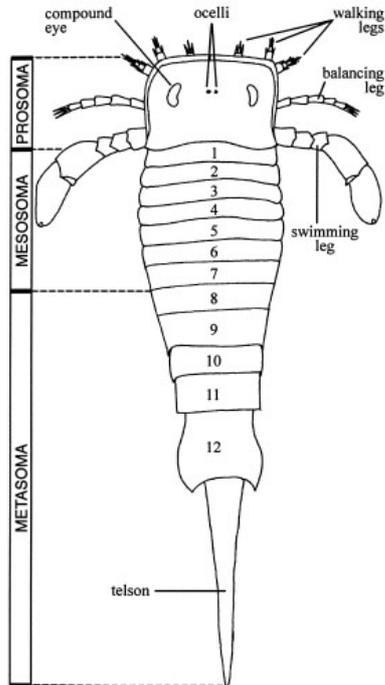


Fig.2. Body plan of *Eurypterus* (modified, Donovan 2001)

Hypothesis on eurypterid environments

Based on the evaluation of the paleoecology of all known eurypterids Braddy (2001) has summarized and discussed the following hypotheses known so far and proposed a new concept:

The “**river hypothesis**” suggested by Chamberlin (1900) considered for eurypterid a freshwater environment with an adaption for life in rivers with evidence of terrestrial plants.

The “**transition hypothesis**” of Clarke (1900) proposed that eurypterids have been “originally wholly marine in the Ordovician, inhabited broader salinity regimes in the Silurian and Devonian, being adapted to lagoonal and estuarine environments (as they are commonly found in hypersaline or brackish marginal marine environments), and became confined to brackish and freshwater habitats in the Late Palaeozoic.” (Braddy 2001) “Variations in the distribution of eurypterid fauna between the localities in the Upper Silurian were recognised, with particular species restricted to specific environments.” (Braddy 2001)

Størmer (1934a, 1955) developed the “**hypersaline hypothesis**” concluding eurypterids were tolerant of changeable salinities (Størmer 1934a) and eurypterids lived predominantly in fresh water but occasionally inhabited marine conditions (Størmer 1955) (Braddy 2001).

The “**facies hypothesis**” of Kjellesvig-Waering (1961) recommended three bio-facies reflecting salinity tolerance (see Fig. 3) for the zonal location of these phases. At first there is the Carcinomatidae-Pterygotoides (C/P) phase, which represents the most-marine phase with open marine to brackish water, typical sediments and marine fauna. The second phase called Eurypteridae (E) phase covers “transitional marine to brackish waters, with a tendency to hypersalinity (e.g. sheltered marine bays, nearshore environments, back reef lagoons, estuaries or hypersaline restricted environments, typically with rare marine faunal association)” (Braddy 2001). “Near shore brackish to freshwater habitats” (Braddy 2001) with bays, lagoons and estuaries represent the Hughmilleriidae-Drepanopteridae-Stylonuroidea (H/D/S) phase. Selden (1984) recognised that models like the facies hypothesis only work while the eurypterids demonstrate a life assemblage (Braddy 2001).

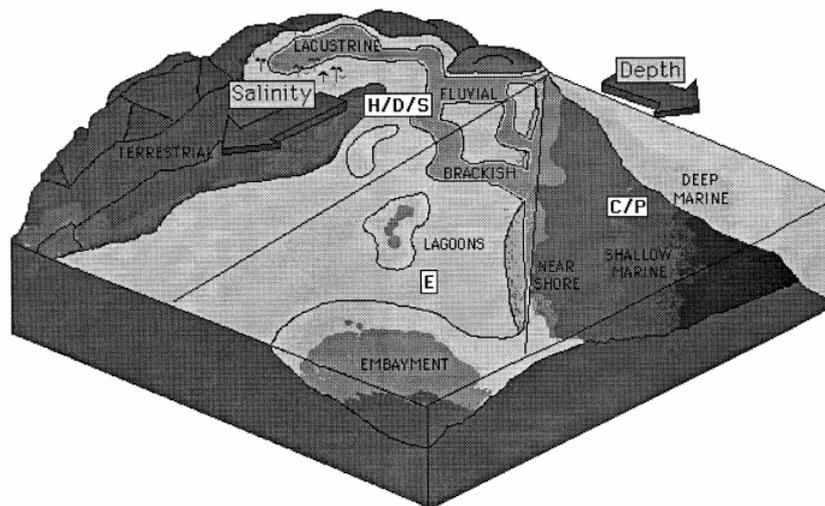


Fig.3. Diagram of the zonal range of facies hypothesis of Kjellesvig-Waering (1961, from Braddy 2001)

Braddy (2001) developed a reworked facies model of eurypterids palaeontology with attention of overlapping of paleoecological range of eurypterid genera, defined of overlapped environmental and palaeobiological criteria. Thereby, the development of the eurypterid respiration and reproduction as the palaeophysiological factors play an important part including an “ontogenetic gradient, whereby juvenile eurypterids preferentially adopted marginal and near-shore habits” (Braddy 2001).

Furthermore a “**mass-moult-mate hypothesis**” is suggested by Braddy (2001) based on the discovery of shallower marginal, near- shore environments of juveniles and the dominance of adults in marine sequences. Also Manning (1993, unpublished) supposed an ontogenetic segregation of adults and juveniles of the Welsh Borderlands eurypterids. Segregation would have guaranteed less competition among juveniles and adults. The choice of mudflats, sandbars etcetera, laying for deposition of eggs distantly from aquatic predators would have increased the survival chances of juvenile eurypterids just as have protected the juveniles from possibly cannibalism (Selden 1984). The visiting of the shore and laying their eggs there was first noted by Ruedemann (1934). Størmer (1976) suggested a deposition of eggs in near shore areas of the water, intertidal zones and lagoons from where the eurypterids even crawled up to the beach. Briggs and Rolfe (1983) also supposed a nuptial walk for eurypterids and Caster and Kjellesvig-Waering (1964) noted a probably need of quiet free area for moulting (Braddy 2001).

The “**mass-moult-mate hypothesis**” (Braddy 2001) assumes that eurypterids “synchronised their moulting and mating behaviour, migrating en- masse into near shore or quiet water lagoons to moult and mate before returning to their usual habitats”. This is promoted also by sub-parallel eurypterid trackways of variously size found from time to time along fossil coastlines (Braddy 2001). Further evidence came from dual respiratory system of eurypterids which comprised of “four pair of vertical lamellate book-gills, housed within the branchial chambers, for aquatic respiration (Braddy et al. 1999) and “Kiemenplatten, situated above the gills, which are interpreted as accessory aerial respiratory surfaces” (Selden 1985, Manning and Dunlop 1995).

Braddy (2001) provides additional examples of different locations to accentuate his conclusions. Clarke and Ruedemann (1912) noted “variations in species and sizes” of eurypterid of Upper Silurian Bertie Formation at Buffalo, New York State, USA (Braddy 2001). This occurrence of “larger species from the Buffalo sequence and the smaller size and apparent abundance of juveniles characterising the Herkimer County species” (Braddy 2001) was interpreted by Clarke and Ruedemann (1912) as a paleocological separation perhaps caused by variations in water depth and salinity. Sequences where the eurypterids were found are interpreted as been a subtidal (Hamell 1982), “near shore lagoon showing fluctuating salinity” (Heckel 1972, Copeland and Bolton 1985) to “brackish to freshwater lagoon or estuarine” (Kindle 1934) (Braddy 2001). The Bertie Formation assemblage is discussed to have been at least partly moults although it seems to have been a mass death assemblage (Andrews et al. 1974). However Braddy (2001) arguments that the fact of having many growth stages could be equally declare that whole population did mass moulting.

Late Palaeozoic eurypterids and their environments – the facts

Superfamily HIBBERTOPTEROIDEA Kjellesvig-Waering 1959

Family: Hibbertopteridae Kjellesvig-Waering 1959

Genus: Hibberopterus Kjellesvig-Waering 1959
and

Family: Cyrtcoctenidae Waterston et al. 1985

Genus: Cyrtcoctenus Størmer and Waterston 1968

Dunsophterus 1968, possibly cogenetic (Waterston et al. 1985)

The Viséan, Early Carboniferous, *Hibberopterus* from East Kirkton, Scotland, is discussed by Waterston (1957) and Waterston et al. (1985) as having “raked trough soft sediments for shallow fauna” which could be swept into the mouth instead of having been a “predator of relatively large animals” because of the amount of sense organs at the first pairs of appendages, the weakly development of the chelicerae and coxal gnathobases (**Jeram and Selden 1994**). It is discussed that *Hibberopterus* showed some terrestrial adaptations (Rolfe 1986) and indicated terrestrial activity (Selden 1984, 1985) while Waterston et al. (1985) inferred for *Cyrtcoctenus* an aquatic environment. Further evidence for the terrestrial activity is that it seems that “the eurypterids did not breeding in the East Kirkton lake” suggesting that “the eurypterids were not permanent inhabitants of the lake” (Jeram 1994). The absence of juvenile suggests that the nursery pool were outside the East Kirkton lake (Jeram and Selden 1994) and the adults had the potentiality to walk there on land. The East Kirkton lake had been situated at the paralic near shore zone.

Superfamily: EURYPTERACEA Burmeister 1845

Family Hughmilleridae Kjellesvig-Waering 1951

Genus: Adelophthalmus Jordan and von Meyer 1854

The Virgilian, possibly Early Wolfcampian, Early Permian, *Adelophthalmus* from northern end of the Lucero Mountains along Carrizo Arroyo, central New Mexico, USA, seems to be approximately non-marine. **Kues and Kietzke (1981)** described the environment as having been “in and around bodies of brackish to fresh water on a deltaic plain with ponds or lagoons”. Krainer and Luca (2004) suggested a “freshwater lake on a coastal flood plain” (Johnson and Lucas 2004). In the “Major Eurypterid Zone” there is also a “well preserved flora consisting of ferns, fern like plants including Callipteris and Gymnosperms like Cordaites and Walchia” suggesting a deposition in quiet conditions while small eurypterids are found in beds having less small plant fragments indicating a deposition in low areas on the delta plain between ponds and neighbouring distributaries through which floodwater sluggish flowed (Kues and Kietzke 1981). The abundance of *Cordaites* should indicate proximity to marine conditions (Phillips et al. 1974) just as the two limestone conglomerate beds which contain fragments of marine invertebrates which suggest that storms sometimes flooded the delta plain with marine material (Kues and Kietzke 1981). It is more believable that juveniles lived or were preserved in somewhat different environment than the adults (because there is only a small number of juveniles in the “Major Eurypterid Zone”) (Kues and Kietzke 1981), than that the small number of juveniles result from cannibalism as documented in Ordovician forms by (Caster and Kjellesvig-Waering 1964).

Kues and Kietzke (1981) suggest for the segregation of adults and juvenile eurypterids that the adults lived concentrated in ponds where salinity was somewhat variable, while the juveniles lived in fresher and less variable waters further from the shoreline. They determine that the adults perhaps mated and produced offspring in the streams that fed the ponds, but returned to spend their lives in the ponds because of the richer food supply there. Segregation of adults and juveniles among arthropods is not uncommon (Andrews et al. 1974).

The Late Wolfcampian, Early Permian, arthropod trackways of several localities at the Robledo Mountains, New Mexico, “indicate a diverse aquatic and subaerial community” including myriapods, scorpions, spiders, eurypterids (*Palmichnium*), xiphosurans, crustaceans, and several different types of insects (Braddy 1995, 1998; Kozur and Lemone 1995) (Braddy and Briggs 2002). “Mud cracks and rain prints, sometimes preserved alongside the traces, indicate subaerial conditions, but ripple marks preserved on other surfaces, indicate that exposure was intermittent, perhaps as part of a tidal flat, inferred on sedimentary structures and the palaeogeographic setting” (Lucas et al. 1995). The Hueco Formation shows non-marine red bed and depositions of the intertidal, which are “truncated by, or grade laterally into, rare channel sandstones, which represent tidal-creek or estuarine facies” (Mack and James 1986). Plant fragments (*Walchia*), which indicate an at least partly vegetated palaeo-coastline, are quite common (MacDonald 1992).

Superfamily: EURYPTERACEA Burmeister 1845

Family: Hughmilleridae Kjellesvig-Waering 1951

Genus: *Adelophthalmus* Jordan and von Meyer 1854

The Late Carboniferous *Adelophthalmus* from the coal mine “Minister Stein”, Dortmund, the coal mine Friedrich Thyssen, Duisburg, and from coal mine Wilhelmine-Victoria, Gelsenkirchen, all from the Ruhr district, Germany, are all non-marine (Schwarzbach 1962). The deposition environments of Bochum strata (Westphalian A) and Essen strata (Westphalian B) where the eurypterids have been found are all non-marine sequences what is conform to knowledge about the “Upper Carboniferous merostomata which are supposed to had lived nearly all in freshwater” (Schwarzbach 1962). But it has to be taken into account that the Ruhr district belongs to the Variscan paralic foredeep.

Superfamily: EURYPTERACEA Burmeister 1845

Family: Hughmilleridae Kjellesvig-Waering 1951

Genus: *Adelophthalmus* Jordan and von Meyer 1854

The publication of Brauckmann (2005) is a summary of selected Late Carboniferous arthropods of Middle Europe. It is noted by Brauckmann (2005) that there are only a few eurypterids found in Germany especially in the Saarland (Westphalian D) (Waterlot 1934) in the Ruhr district (Westphalian A and B) (Schwarzbach 1962, Brauckmann 1991a) and in Hagen-Vorhalle (Namurian B) (Brauckmann 1988, Brauckmann et al. 2003) also in the Ruhr district. The Saar basin is known as a non-marine intra-mountainous basin. That means the eurypterids liv-

ing there should be non-marine too. The Ruhr district instead is part of the paralic sub-variscan foredeep basin which is influenced by short-termed marine incursions.

Superfamily: EURYPTERACEA Burmeister 1845

Family: Hughmilleridae Kjellesvig-Waering 1951

Genus: *Adelophthalmus* Jordan and von Meyer 1854, no confident determination possible

Adelophthalmus described by **Kues (1988)** from the Upper Pennsylvanian Hamilton Quarries, Kansas, USA, seem to have lived in a non-marine environment. The limestone bearing the eurypterids is supposed to be a “part of a channel deposit”, nearly all organisms (insects, myriapods, plants) preserved in this limestone are terrestrial and remains of marine organisms are very rare and highly fragmented so that a assumption of a approximately non marine, “generally quiet water body” is not far (Kues 1988). Some specimens nearly show no transportation and thus it is very likely that the environments of the deposition of the limestone is “also the environment where the eurypterids lived” (Kues 1988). Kues (1988) noted that there have been also found unornamented ostracods. “Ostracods are the dominate microfossils in fresh and brackish environments dating back to the Pennsylvanian, may contribute significantly to the volume of sediments in some brackish lagoons, and generally are characterized by an increase in smooth forms relative to ornamented types as salinity declines from 35‰” (Benson 1961).

Superfamily: HIBBERTOPTEROIDEA Kjellesvig-Waering 1959

Family: Hibbertopteridae Kjellesvig-Waering 1959

Genus: *Hibberopterus* Kjellesvig-Waering 1959

Whyte (2005) described an Asbian, Early Carboniferous, *Hibberopterus* trackway from Scotland which is the “first record of locomotion on land for a species of *Hibbertopterus*” which showing a “lumbering movement” indicating a survival out of water. The trackway (Fig. 4) is on a “bedding plane close to the base of a sandstone in a non marine sequence” (Whyte 2005).



Fig.4. eurypterid trackway, Early Carboniferous, Scotland, (from <http://news.bbc.co.uk/1/hi/sci/tech/4486830.stm>)

Schwarzbach (1957) described a Namurian eurypterid from marine horizon III of the Deutschlandgrube, Upper Silesia, Poland, deposited together with *Lingula*, which occurs also in brackish water. A further definition is not possible, because the fossil got lost in 1945 but there is a photo in the possession of the author (Schwarzbach 1957). Furthermore there is a *Stylonurus?* from Ostrau, Upper Silesian Central Coal Field, Poland, which occurred with lots of marine molluscs, gastropods and trilobites (Schwarzbach 1957). It is noted that the eurypterids from the Upper Silesia are older than these from the Netherlands and from Westphalia, Germany, and it is possible that the questionable transfer from marine into limnic environments occurred in the Late Carboniferous (Schwarzbach 1957). The author noted that there is further material required because of the possibility that the fragments have been washed in the marine environment (Schwarzbach 1957).

Superfamily: EURYPTERIDA Burmeister 1843

Family: Hughmilleriidae Kjellesvig-Waering 1951

Genus: *Adelophthalmus* Jordan and von Meyer 1854

Scott (1971) described a eurypterid of the Pennsylvanian to Permian Dunkard Group, western Pennsylvania, USA, especially from the Cassville Shale which is interpreted to have been a lacustrine or floodplain deposit not far away from a sea-way.

Falcon-Lang et al. (2006) mentioned from the Pennsylvanian Joggins Formation, Chignecto Bay, Nova Scotia, Canada, eurypterids within the retrograding and prograding “poorly drained coastal plain fossil assemblage” (Falcon-Lang et al. 2006).

The Joggins Formation is built of 14 rhythms, (Davies and Gibling 2003, Davies et al. 2005) which are composed among others of “a retrograding, poorly drained coastal plain association” (Falcon-Lang et al. 2006), where fragments of *Hastimima*, a giant eurypterid, (Clarke and Ruedemann 1912, Bell 1922, Copeland

and Bolton 1960, Briggs et al. 1979, Waterston et al. 1985) have been found. This “retrograding, poorly drained coastal plain association” is “typically overlain by an open water association” signifying a brackish water flooding into the basin (Falcon-Lang et al. 2006). The following strata is the “prograding poorly drained coastal plain fossil assemblage” with eurypterid fauna “comparable with *Dunsop-terus*, *Hibbertopterus*, *Vernonopterus*” (Waterston 1968) or *Mycterops* (Dalingwater 1975, Briggs et al. 1979, Rolfe 1980), interpreted as wetland and delta bay-filling (Falcon-Lang et al. 2006). Rainforests with lycopsids, pteridosperms, cordaitaleans and ferns covered the coastal plains which were inhabited by “terrestrial fauna of molluscs, annelids, arthropods, and tetrapods, including the earliest known reptiles” (Falcon-Lang et al. 2006).

The Joggins Formation is quite significant in comparison to other Pennsylvanian sites because it “is located further inland” and “contains a record of intra-continental terrestrial ecosystems” (Falcon-Lang et al. 2006).

Early Palaeozoic eurypterids and their environments

Tetlie (2006) describes the location Herefordshire, Welsh Borderlands, England, with two Pridolian, Late Silurian (Plotnick 1999), assemblages (modified from Bassett et al. 1982) from Downton Castle Sandstone Formation and Temeside Shales Formation which contain the following organisms:

Erettopterus brodiei, *E. spatulatus*, *Eurypterus cephalaspis*, *Nanahughmilleria pygmaea*, *Slimonia* (?) *stylops*, *Marsupipterus sculpturatus* and *H. banksii*. *Dolichopterus bulbosus*, *E. spatulatus*, *Truncatiramus gigas*, *Pterygotus ludensis*, *Parahughmilleria salteri*, *Salteropterus abbreviatus* and *Hardieopterus megalops*.

Both benthic assemblages show intertidal sandy shore and intertidal sandy mudflat environments (Plotnik 1999). Braddy (2001) noted that this assemblage of the Welsh Borderland has been represented as an example of the “H/D/S phase” of the facies hypothesis by Kjellesvig-Waering (1961).

The trace fossil *Palmichnium stoermeri* from basal Sundvollen Formation of the Late Silurian Ringerike Group of southern Norway which is a “deposition in a number of sub-environments of a broad, muddy coastal-plain setting” (**Davies et al. 2006**) is interpreted as a large trackway of the eurypterid *Mixopterus* (Hanken and Størmer 1975, Briggs and Rolfe 1983). “This offshore sedimentation is thought to have taken place in a shallow epicontinental sea” (Dam and Andreassen 1990). Despite the deposits that constitute this environment being fluvial derived, there is no evidence for this nearshore sequence being deltaic, so the depositional system is considered to be a broad, alluvial coastal plain (Davies 2003, Halvorsen 2003). The association into which *Palmichnium* occurs is situated “in the most marine of the Sundvollen paleoenvironments, occurs in red siltstones showing no signs of subaerial exposure” and represents “the most marginal marine intertidal portion of the overall coastal-plain environment” (Davies et al. 2006).

Superfamily: Stylonuracea Diener 1924

Family: Rhenopteridae Størmer 1951

Genus: Rhenopterus Størmer 1936

The Frasnian, Upper Devonian, Rhenopterus from the Gogo Formation of Western Australia, occurs together with a diverse fauna (sponges, brachiopod, ammonoids (Glenister 1958) etcetera) and is supposed to be marine but it is only a single eurypterid which probably could be “transported into this fully marine environment” (Tetlie et al. 2004). Further eurypterid trace fossils have been noted “from the late Silurian Tumblagooda Sandstone of Kalbarri in the Murchison district of Western Australia” (Trewin and McNamara 1995). One of the trackways from the Tumblagooda Sandstone has been interpreted as subaerial (Trewin and McNamara 1995) and it seems that the eurypterid used “a lurching, in-phase gait, suggesting that the animal was poorly adapted for walking on land” (Briggs et al. 1991).

Superfamily: HUGHMILLERIOIDEA Kjlesvig-Waering, 1951

Family: Hughmilleroides? / Carcinomatidae?

Genus: Orcanopterus

Stott et al. (2005) described a new species of eurypterid from the Upper Ordovician of Manitoulin Island, Ontario, Canada and the environmental is discussed has been marine, shallow subtidal to intertidal with restricted marine lagoons. The assemblage represents perhaps “an accumulating of moulted exuviae (which) was apparently preserved as the result of rapid burial by carbonate muds and silts during a storm event” (Stott et al. 2005).

Did special eurypterid groups have had special environments?

For this question it is possible to look at the following tables (table 1 and 2) where the Hughmilleridae especially *Adelophthalmus* and Hibbertopteridae (*Hibbertopterus*) apparently favoured fresh to brackish water habitats. Further correlations are not yet possible because additional material should be analyzed concerning special environments of special eurypterid families.

author	Family/ Genus	environment	facies pattern
Kues and Kietzke (1981)	Hughmilleridae/ <i>Adelophthalmus</i>	non-marine	brackish to freshwater, ponds, lagoons, “fresh-water lake on a coastal flood plain”
Schwarzbach (1962)	Hughmilleridae/ <i>Adelophthalmus</i>	non-marine	
Brauckmann	Hughmilleridae/	non-marine	(Saar basin: non-marine)

(2005)	<i>Adelophthalmus</i>		intra-mountainous basin, Ruhr district: paralic)
Kues (1988)	Hughmilleridae/ <i>Adelophthalmus</i>	non-marine	quiet waterbody, channel fill
Scott (1971)	Hughmilleridae/ <i>Adelophthalmus</i>	non-marine	lacustrine or floodplain deposit, not far from seaway
Jeram and Selden (1994)	Hibbertopteridae/ <i>Hibberopterus</i>	non-marine	lacustrine (“East Kirkton Lake”)
Whyte (2005)	Hibbertopteridae/ <i>Hibberopterus</i> trackway	non-marine	
Falcon-Lang et al. (2006)	<i>Hastimima</i> , <i>Dunsopterus</i> , <i>Hibberopterus</i> , <i>Vernonopterus</i>	non-marine	terrestrial wetlands, delta bay, brackish water
Jeram and Selden (1994)	Cyrcocotenidae	non-marine	lacustrine (at a paralic near shore zone)
Braddy and Briggs (2002)	trackway of eurypterid (<i>Pal-michnium</i>)	non fully marine	intertidal, tidal creek, estuarine
Schwarzbach (1957)	undefined eurypterid and <i>stylonurus</i> ?	marine?	only a single eurypterid, there is further material required because of the possibility that the fragments have been washed in the marine environment (Schwarzbach 1957)

Table 1. designated environments of Late Palaeozoic eurypterids

author	Family/ Genus	environment	facies pattern
Tetlie (2006)	<i>Eurypterus</i> , Nana- and Para-Hughmilleridae	marine	intertidal sandy shore, intertidal sandy mudflat
Davies et al.	trackway of	marine	shallow, most marine

(2006)	<i>Mixopterus</i>		intertidal area
Tetlie et al. (2004)	trackway of <i>Rhenopterus</i>	marine	together with marine fossils, but it is only a single eurypterid
Stott et al. (2005)	<i>Orcanopterus</i>	marine	shallow subtidal to intertidal, restricted marine lagoons

Table 2. designated environments of Early Palaeozoic eurypterids

Conclusions

Resulting from the data summarized above, no general answer could be given to the question for the environment preference of eurypterids. But if we divide the eurypterids into Early and Late Palaeozoic forms it appears that all of the Early Palaeozoic eurypterids seem to be marine. The Late Palaeozoic eurypterids have a wide ecological range from marine brackish to non-marine lacustrine environments with at least proximity to a marine shore.

Buatois et al. (2005) suggested for the Silurian-Carboniferous brackish water colonization phase that a “widespread colonization of continental environments by land plants and animals likely promoted environmental expansion and complexity of estuarine food webs”.

The ability of terrestrial walks did not force to fundamental changes of environments throughout the Late Palaeozoic otherwise does such terrestrial walks require a certain tolerance and adaption. So it is not surprising that eurypterids primary settled to brackish and freshwater environments. The question if the wholly marine environment had been quitted in the Late Palaeozoic could have an affirmative reply because there is probably no evidence of a totally marine Late Palaeozoic eurypterid except for Schwarzbach (1957) who described a marine Late Carboniferous eurypterid from Upper Silesia. Apart of that he noted it could be perhaps washed in from limnic environment into the marine deposits.

Plotnick (1983 unpublished) noted that no deep shelf condition eurypterid locality is known after the Emsian, Early Devonian (Braddy 2001).

Otherwise there is a tolerance against marine influence and salinity at the new occupied habitats. There are diverse opinions about the ability of eurypterids to tolerate differences of salinity. While Heckel (1972) as well as Copeland and Bolton (1985) interpret the environment of eurypterids of the Bertie Formation, Upper Silurian of Buffalo, New York State, USA, as “a near shore lagoon showing fluctuating salinity” Plotnick (1983 unpublished, 1999) noted in general “no evidence that eurypterids were euryhaline” (Braddy 2001).

Caster and Kjellesvig-Waering (1964) suggested with reference to their facies hypothesis an extinction of the Carcinosomatidae-Pterygotoides (C/P) phase (open

marine) and Eurypteridae (E) phase (transitional marine to brackish) eurypterids during the Devonian while all subsequent animals belonged to the Hughmilleriidae-Drepanopteridae-Stylonuroidea (H/D/S) phase which represents brackish to freshwater conditions (Braddy 2001).

Anymore there are only a few proofs of wholly terrestrial (without marine influence) environments where Late Palaeozoic eurypterids occurred. One Example is the non-marine intra-mountainous Saar basin, Germany, where Brauckmann (2005) mentioned the evidence of eurypterids. Perhaps this could force to supposition the Westphalian Saar basin could have had an influence of the shore.

It is likely that there has been a transition of the eurypterids from nearly wholly marine to non-marine environments around the Early/Late Palaeozoic boundary.

Bambach (1999) noted: “during the Devonian, relatively sluggish, low metabolic rate (marine) predators were replaced by generally more active taxa with greater overall energy needs. Nautiloids, eurypterids, and asteroids decreased in diversity as ammonoids, malacostracans, and jawed fishes increased.” Which probably consequent of “increased marine productivity and increased energetics in the marine fauna” (Bambach 1999). This replacement of predators as well as the better food supply of fresh and brackish near shore environment and protection against other predators could have forced eurypterids to the transition from wholly marine to brackish-marine and freshwater environments.

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