

The late Middle Devonian fauna of Red Hill I, Nevada, and its paleobiogeographic implications

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Abstract

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The fauna of the Middle Devonian Red Hill I locality, Nevada, is unusual in the co-occurrence of a rich fish assemblage with a rich invertebrate one. Sponges are second in abundance of specimens and number of species only to the fishes and occur together with other invertebrates (conodonts, conulariids, dacryoconarid tentaculites, gastropods, bivalves, brachiopods, arthropods, and unidentifiable ammonoids and echinoderms). The invertebrates indicate a marine depositional paleoenvironment. The conodonts indicate a placement within the lower *disparalis* Zone, late Givetian. The fish assemblage is dominated by the antiarch *Asterolepis*. All the other fishes, acanthodians, actinopterygians and sarcopterygians, are less common. The closest biogeographic relationship of the fish fauna is with the Middle/Late Devonian fish fauna of the Baltic Region, followed by that of eastern Canada (Miguasha), Scotland and Iran. This distribution corresponds to the Devonian Euramerica faunal province with connection to eastern Gondwana (Iran and Australia). Localities with the same genera as Red Hill I are interpreted as marine with the exception of the Scottish localities. *Asterolepis* is the most widely distributed vertebrate genus, mostly marine, but it may be able to enter freshwater like *Eusthenopteron* if one accepts a freshwater depositional paleoenvironment for the Scottish localities.

Key Words

Paleozoic
Givetian
Euramerica
faunal province
paleoenvironment

Introduction

Red Hill I forms the northern end of the Northern Simpson Park Range, northwest of Eureka, Nevada. The Red Hill I locality (lowest part of Red Hill section II in Murphy et al. 1976, Red Hill I of Gregory et al. 1977) lies near the exposed bottom of a sequence of reddish, yellow and greenish gray silty lime mudstones, approximately 80 m thick, at the base of the southwest flank of Red Hill (NW ¼, NE ¼, section 17, T.25N, R.50E on the Horse Creek Valley 15-Minute Quadrangle in Eureka County, Nevada; or 40°03'3" N and 116°02'07" W at about 2070 m [approximately 6220 ft.] above sea level).

The locality was discovered by Michael Murphy from University of California, Riverside, California, in 1973. The most common fish, *Asterolepis*, was first described by Murphy et al. (1976). J. T. Gregory and his student J. Reed from University of California, Berkeley, California, continued the excavations in 1974 and 1975, and J. T. Gregory with another Berkeley crew in 1984.

In 1979 J. Reed completed a Ph.D. thesis on *Asterolepis* that was never published; he did publish on other fish though (Reed 1985, 1986, 1992). A crew from the University of Kansas excavated in the years between 1981 and 1987: in 1983 together with one German volunteer (P. Brühn) and systematically layer by layer (Fig. 1) in 1987 together with two German volunteers (P. Brühn and E. Thomas).

Stratigraphy

The fish-bearing section starts 3–4.5 m above an intraformational conglomerate within the Red Hill Beds and about 80 m below the Devils Gate Limestone. The Red Hill Beds form an 80 m thick intercalation between the Denay Limestone below and the Devils Gate Limestone above. The Middle/Late Devonian boundary lies within the Red Hill Beds just above the fish beds. The fishes occur in a little over 1.5 m thick sequence of well-bedded lime mudstones (Fig. 1). Thicker bedded lime-

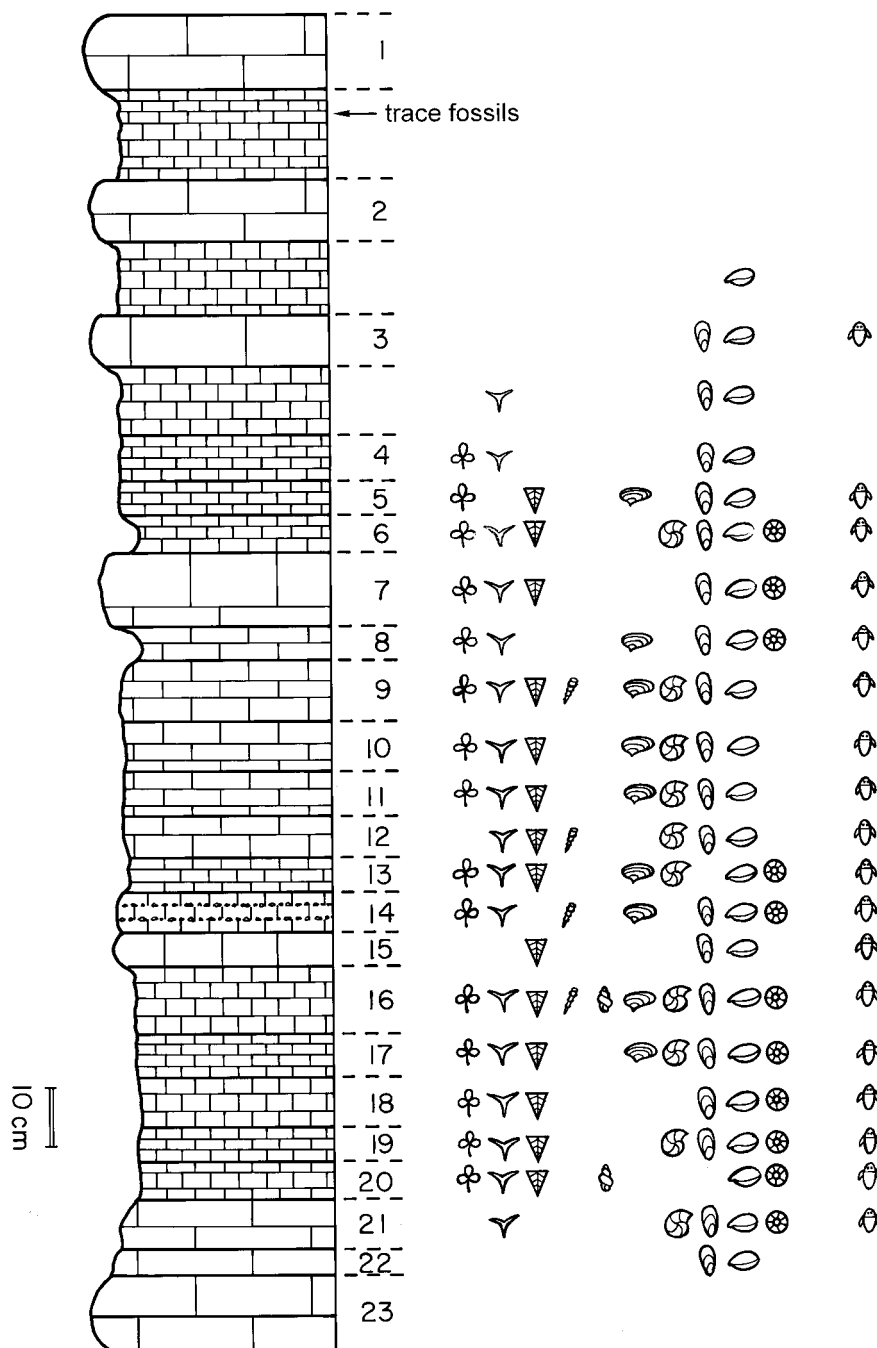


Figure 1. Section of the fish horizons in the thin-bedded lime mudstones alternating with thick-bedded limestones of the Red Hill Beds, Middle Devonian at Red Hill I, Nevada (Middle/Upper Devonian boundary above the section). Symbols from left to right: plants, invertebrates (sponges, conulariids, dactyloconarids, gastropods, bivalves, ammonoids, lingulids, articulate brachiopods, echinoderms) and fishes.

stones are intercalated within the finely bedded sequence. Two bone beds occur in layer 14. The layers were numbered from the top down as the excavation progressed. On the right side of the section (Fig. 1), the symbols show the distribution of the fauna. Here we have the unusual situation that a rich fish fauna occurs together with a rich marine invertebrate fauna.

In the literature, different biostratigraphic ages are given for the fish-bearing section, and this has historical reasons. A consensus on the position of the Middle/Late Devonian boundary was reached in the 1980s. Therefore the placement of the Red Hill I fish beds into the earliest Late Devonian (Johnson 1977: *Leiorhynchus hippocastanea* Zone [brachiopod interval 25]

corresponding to earliest *Polygnathus asymmetricus* Zone [conodont]) corresponds to the placement of the boundary below the *P. asymmetricus* Zone. Gregory et al. (1977) and Reed (1985, 1986) supported the early Late Devonian age by comparison with Baltic fish occurrences in the Gauja and Amata beds. With the placement of the Middle/Late Devonian boundary above the earliest *P. asymmetricus* Zone, the fish occurrences were moved into the latest Givetian (Johnson et al. 1988). Murphy et al. (1976) had already given a late Middle Devonian age (upper *Schmidtofnathus hermanni-Polygnathus cristatus* Zone). The conodonts occurring with the fish indicate a placement within the early *Klapperina disparalis* Zone, latest Givetian (Johnson

1990, fig. 52; Elliott & Johnson 1997; Elliott et al. 2000), which corresponds to the present day placement of the Middle/Late Devonian boundary.

Institutional abbreviations. KUMIP – Invertebrate Paleontology collections, and KUVP – Vertebrate Paleontology collections, Natural History Museum & Biodiversity Research Center, The University of Kansas, Lawrence, Kansas; USNM – U.S. National Museum, Washington D.C., USA.

Fossil assemblage

The fossil assemblage is unusual among rich fossil fish localities as also being rich in sponges, conulariids, articulate brachiopods, and echinoderms. Plants, gastropods, ammonoids, inarticulate brachiopods and echinoderms are so poorly preserved that they are unidentifiable. Sponges are the most common fossils next to the fishes; the sponge fauna is diverse with 16 different forms. Sponges and conulariids, like most invertebrates and fishes, are flattened; they are preserved, at least in part, with hematite. The change to hematite probably occurred during a widespread hydrothermal event within the region during the Tertiary (Johnson 1960; McKee 1996; Tingley & LaPointe 1997); that event is responsible for the red color of the sediments. The locality lies within the Battle Mountain – Eureka Trend (French et al. 1996, fig. 3) northeast of the Tonkin Springs mine. Ore deposits and hydrothermal changes of sediments are connected with the intensive fault systems. The age for the hydrothermal event is given as after Miocene basaltic andesites (16.9 ± 0.2 Ma) for the Buckhorn district (Benedict 1996) northwest of Red Hill I or after the late Oligocene magmatic event (24–25 Ma) for the Gold Bar district in the Roberts Mountains (French et al. 1996) southeast of Red Hill I or even earlier (36–38 Ma) after Ressel (2005; Cellura personal comm.).

The co-occurrence of abundant sponges and fishes is most unusual. J. K. Rigby visited the quarry during the 1987 excavation by the Kansas University crew and later described many new sponge genera and species together with D. Mehl (Rigby & Mehl 1994). The articulate brachiopods were described by Johnson (1978), and the conulariid was described by Babcock & Feldman (1986a).

Flora and invertebrate fauna of the Red Hill I beds, Nevada

Plants (letter from P. G. Gensel, Department of Biology, University of North Carolina, Chapel Hill, North Carolina, 14.8.1992):

“pieces of algae resemble charophytes – could be *Chara* or *Nitella*” (levels 4–11, 13, 14, 16–20)

Trace fossils (identified by F. Langenstrassen, Institut für Geologie und Paläontologie, Georg-August-Universi-

sität, Göttingen, Germany, 18.11.1987):

?*Thalassinoides* or ?*Quebecichnus*

“Invertebrates”

Porifera (Rigby & Mehl 1994):

Hexactinellida

Order Reticulosa

Family Protospongiidae

Actinodictya nevadensis Rigby & Mehl, 1994

(levels 5, 10, 16)

Actinodictya lamina Rigby & Mehl, 1994

(levels 10–11, 19)

Protospongia conica Rigby & Harris, 1979 (level 10)

Family Dictyospongiidae

Cyathophycella minuta Rigby & Mehl, 1994

(level 21) (Fig. 2)

Cyathophycella grossa Rigby & Mehl, 1994 (level 16)

Dictyospongia(?) robusta Rigby & Mehl, 1994

(levels 19–20)

Dictyospongia(?) amplia Rigby & Mehl, 1994

(level 19)



Figure 2. Holotype of the sponge *Cyathophycella minuta* Rigby & Mehl, 1994 (USNM 463531, compare Rigby & Mehl 1994, pl. 4, fig. 11). Lower *disparalis* Zone, latest Givetian; Red Hill I, northern end of the Northern Simpson Park Range, northwest of Eureka, Nevada.

Family Hintzespongiidae

Cyathophycus simpsonensis Rigby & Mehl, 1994
(levels 4, 6–7, 9)

Family Teganiidae

Bulbospongia bullata Rigby & Mehl, 1994
(levels 16, 18–19, 21)

Rufuspongia triporata Rigby & Mehl, 1994
(levels 6–8, 11–13)

Rufuspongia sp. (level 19)

Taleolaspongia modesta Rigby & Mehl, 1994
(levels 2, 7, 12, 18–19, 21)

Teganiella ovata Rigby & Mehl, 1994
(levels 6–7, 9–11, 17–19)

root tuft A (level 5)

root tuft B (levels 6–8, 10)

root tufts C (levels 8–9, 18)

Conulariida (Babcock & Feldmann 1986a):

Paraconularia recurvatus Babcock & Feldmann, 1986a
(levels 5–7, 9–13, 15–20) (Fig. 3)

Cnidaria:

alveolitid tabulate corals

Dacryoconarida:

(levels 9, 12, 14, 16)



Figure 3. The conulariid *Paraconularia recurvatus* Babcock & Feldman, 1986a (KUMIP 314320). Lower *disparilis* Zone, latest Givetian; Red Hill I, northern end of the Northern Simpson Park Range, northwest of Eureka, Nevada.

Gastropoda:

unidentified (levels 16, 20)

Bivalvia (identified by J. B. Bailey, Dept. of Geology, Western Illinois University, Macomb, Illinois, June 1988):

probable nuculid (level 8)

Buchiola sp. (level 8)

Praecardium sp. A (levels 8–9)

Praecardium sp. B (level 9)

Solemya (?*Janeia*) sp. (level 9)

Modiella sp. (levels 9, 14)

Ammonoidea (identified by M. S. Peterson, Dept. of Geology, Brigham Young University, Provo, Utah, 27.4.1995):

Unidentifiable specimens [clymenids]

(levels 6, 9–13, 16–17, 19, 21)

inarticulate Brachiopoda:

unidentified (levels 3–12, 14–19, 21–22)

articulate Brachiopoda (identified by the late J. G. Johnson, Dept. of Geology, Oregon State University, Corvallis, Oregon, 17.12.87: levels 9, 11–12, 14, 16–18; Johnson 1978, 1990):

Leiorhynchus hippocastanea (Crickmay, 1960)

Ladjia russelli (Johnson, 1978)

Vallomyonia claudiae Johnson, 1978

Echinodermata:

unidentifiable stem pieces (levels 6–8, 13–14, 16–21)

Conodonts (identified by M. Murphy, Dept. of Geology, University of California, Riverside, California, 15.10.1992):

Polygnathus cristatus Hinde, 1879

(cited in Murphy et al. 1976)

Klapperina (*Palmatolepis*) *disparilis*

(Ziegler & Klapper, 1976 in Ziegler et al. 1976)

(cited in Johnson 1978)

Polygnathus foliatus Bryant, 1921

(cited in Gregory et al. 1977)

Polygnathus ordinatus Bryant, 1921

(cited in Gregory et al. 1977)

Schmidtognathus spp. (cited in Gregory et al. 1977)

Dacryoconarid tentaculites are poorly preserved. Gastropods, bivalves and ammonoids are difficult to identify, and ammonoids cannot be identified even to group, whereas the brachiopods have been used for stratigraphic determination. For echinoderms, only pieces of the stem have been found. Three three-dimensionally preserved specimens of a tabulate coral are kept in the collections of the Museum of Paleontology, Berkeley. The conodonts, like the brachiopods (*Leiorhynchus hippocastanea* Zone), give an exact age for the deposits. Conulariids and hexactinellid sponges are unusually abundant in the Red Hill I Lagerstätte; they occur in close association with fish throughout most of the quarried section. The sponges are second in number of specimens and species only to the fishes. The co-occurrence of abundant fish and conulariids is known

otherwise only from one Pennsylvanian locality (Muncie Creek Shale Member of the Iola Limestone, Kansas City Group) in Johnson County, Kansas.

Fish assemblage

The most common fish in the Red Hill I Lagerstätte (concentration Lagerstätte in the sense of Seilacher 1970) is the antiarch placoderm *Asterolepis* (Murphy et al. 1976), which occurs disarticulated throughout the section (J. W. Reed described single bones in his Ph.D. thesis 1979). Sometimes complete heads and/or armor, and separate tails of *Asterolepis* occur; one complete specimen with tail (Fig. 4) has been discovered. Os-



Figure 4. The antiarch placoderm *Asterolepis* sp. (KUV 80078A); ventral side. Lower *disparalis* Zone, latest Givetian; Red Hill I, northern end of the Northern Simpson Park Range, northwest of Eureka, Nevada.

teichthyans occur frequently; in descending order of abundance they include lungfish (Reed 1985), rhipidistians and actinopterygians (Reed 1992; Arratia & Cloutier 2004). Arthrodiroids, onychodonts, and acanthodians (Reed 1986) are rare.

The Red Hill I fish fauna (Gregory et al. 1977) is diverse. *Asterolepis*, the most common fish in the Red Hill I Lagerstätte, is the most widely distributed fish genus of the fauna (Schultze & Cloutier 1996). Upeniece (2002) showed a frequent occurrence of *Asterolepis* in Givetian to lower Frasnian localities of the Baltic region, NW-Russia, Timan and Scotland. She also listed occurrences in Belgium, Greenland, Spitsbergen, Iran and the eastern USA. In addition, Denison (1978) cited *Asterolepis radiata* Rohon, 1900 from Kazakhstan and *Asterolepis* sp. from Australia; Young (1993) added one occurrence from the lower Frasnian of New South Wales, Australia; and Janvier & Villarroel (2000) described one from Colombia, South America. Such a worldwide distribution indicates a marine form, which is congruent with the interpretation of the depositional environment of most occurrences (Upeniec 2002) except those in Scotland, Greenland, Spitsbergen and New York State, which are interpreted as freshwater deposits by most authors.

Vertebrates

Placodermi

Asterolepis sp. (levels 3, 5–21): one complete specimen (Fig. 4), heads, trunks, tails, and mainly single plates (Reed 1979)

arthrodire (levels 10–16, 18–19): median dorsal (MD), anterior ventrolateral (AVL), median ventral (MV) plates of coccosteid, suborbital (SO) plate of plourdosteid (Gregory et al. 1977 cite cf. *Coccosteus* and cf. *Plourdosteus*) and anterolateral (AL) plates of pachyosteine arthrodiroids

Acanthodii

Machaeracanthus sp. (level 20): spines (Reed 1986, fig. 1)

Persacanthus simpsonensis Reed, 1986
(levels 10, 14, 17): jaws (Reed 1986, figs 2–6)

Actinopterygii

Cheirolepis schultzei Arratia & Cloutier, 2004
(levels 7–9, 11–12, 14–16, 18–20): anterior body (Arratia & Cloutier 2004, figs 2–4, 5A, 6–8), scales and isolated elements (Reed 1992, figs 1–2; Arratia & Cloutier 2004, figs 1, 9–10).

rhombic palaeoniscoid scales
(levels 6, 8–12, 14–19, 21)

Sarcopterygii

Onychodontida (levels 9, 11, 15–16, 18)
teeth and tooth spirals

Dipnoi

Griphognathus sp.: lower jaw (Reed 1985, figs 3–4)

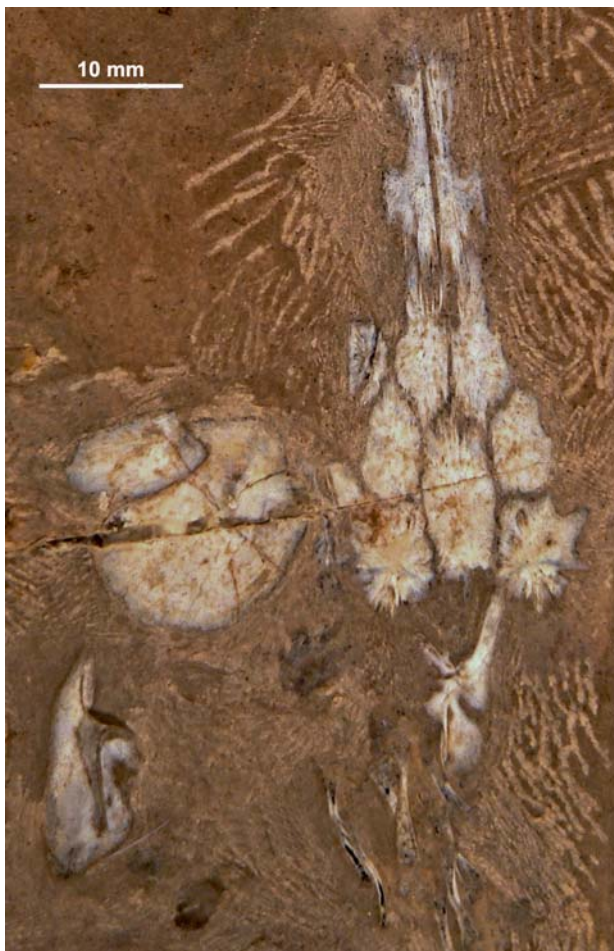


Figure 5. The dipnoan *Soederberghia* sp. (KUVP 93035); skull roof under alcohol. Lower *disparalis* Zone, latest Givetian; Red Hill I, northern end of the Northern Simpson Park Range, northwest of Eureka, Nevada.

Soederberghia sp.: skull roof (Fig. 5)
 dipterid indet. (levels 8–9, 16, 18): tooth plates (Reed 1985, figs 5–7), skull roof bones
 dipnoi indet. (levels 6, 8, 10–13, 16–19): single elements (Reed 1985, figs 1–2, 8–9), nearly complete specimens

Rhipidistia

tristichopterid n. gen. n. sp. (levels 13, 17–18): head (Fig. 6)
 osteolepid indet. (levels 6, 8–21): complete specimens

The new tristichopterid (Fig. 6) is quite closely related to *Eusthenopteron*, if it is placed in the phylogenetic diagram of Ahlberg & Johanson (1997). Shape of lacrimal and jugal, presence of only one supraorbital and the longest preorbital region compared to the skull roof length of all tristichopterids are unique features of the new form. The new tristichopterid has enlarged premaxillary and anterior dentary fangs, a feature typical for advanced (above *Eusthenopteron*) tristichopterids (manuscript in preparation).

Taphonomy

Besides the rare co-occurrence of abundant fish and conulariids, the co-occurrence of abundant fish and glass sponges is exceptional (Rigby & Mehl 1994; e.g. beds 10–12). Fishes, conulariids, and sponges show similar preservation in the Red Hill I Lagerstätte. All have been flattened; it is unusual that all conulariids from a locality are crushed to this extent. Crushing in some conulariid specimens evidently occurred follow-



Figure 6. The tristichopterid rhipidistian n. gen. n. sp. (KUVP 94040); head in left lateral view under alcohol. Lower *disparalis* Zone, latest Givetian; Red Hill I, northern end of the Northern Simpson Park Range, northwest of Eureka, Nevada.

ing initial exoskeletal collapse because some specimens show older, postmortem infolding of the relatively weak exoskeleton in the apertural region. These taphonomically produced structures have been called apertural lappets in the earlier literature (Babcock 1993; Babcock et al. 1987).

Fishes, sponges and conulariids are preserved in various states of disarticulation. Isolated parts of fishes are most common, but sometimes nearly complete specimens can be found (Fig. 4). In addition, fish bone beds have been found in level 14. The sponges are generally fragmented (Rigby & Mehl 1994). However, the presence of complete specimens (Fig. 2) and the presence of seemingly undisturbed thin bedding, together suggests that benthic scavengers and sediment bioturbators are largely excluded from that environment. Rapid and deep burial, dysaerobic conditions, and perhaps hypersaline conditions, are examples of situations that would tend to exclude the scavengers and therefore be conducive to their preservation as fossils. Most conulariids are relatively complete, articulated exoskeletons (Fig. 3) but disarticulated exoskeletal pieces, including individual rods, do occur. The relatively large number of articulated, but not fully complete conulariid exoskeletons contrast with mostly disarticulated specimens of fishes and sponges. The fact that tiny exoskeletal pieces are preserved adjacent to articulated specimens of conulariids and fishes, instead of being washed away, suggests that current agitation and bioturbation of the sediment surface was quite limited except in the bonebeds of level 14. By analogy with the occurrence of disarticulated conulariids in a Mississippian black shale from Ohio (Babcock & Feldmann 1986b), it is inferred that some Red Hill I conulariids were lying on the sediment surface long enough for some disarticulation to occur without interference by currents, benthic scavengers, or sediment bioturbators. Scavengers of conulariids and fishes as well as burrowing organisms, may have been largely excluded from the site of deposition.

There is no indication of disturbance of the specimens after deposition. Thus one has to conclude that the specimens arrived as pieces (disarticulation through decay while floating) or complete at the depositional

site. Marginal disturbance has to be explained by crushing or last forms of decay.

Paleoecology

The invertebrates indicate a marine depositional paleoenvironment. The presence of conulariids in the Red Hill I fauna yields limited paleoecological information because these animals seem to have been rather ubiquitous in many Paleozoic marine habitats (Babcock & Feldmann 1986b). Conulariids are known only from marine strata. *Paraconularia recurvatus* may have been an opportunistic species, as judged by its abundance (conulariids occur usually single or as few specimens), and by the lack of other conulariid species in the fauna. Conulariids as a general rule were evidently capable of tolerating conditions ranging from well-oxygenated to poorly oxygenated (Babcock 1991), and were not restricted by water depth, at least not in shelf seas. Murphy (1977) considered the paleoenvironment of the Northern Simpson Park Range as open marine at the time (also see Rigby & Mehl 1994); Johnson et al. (1988) placed the sedimentation of the limestones on the outer shelf. The trace fossils, which indicate a near shore paleoenvironment, occur only in one horizon above the section with the fish-sponge-conulariid assemblage (Fig. 1).

According to Denison (1978, p. 108), antiarchs are predominantly freshwater stream and lake dwellers, though a few (*Gerdalepis*, *Lepadolepis* and *Grossaspis*) became adapted to marine life. *Asterolepis* is common in coastal marine sediments of the Middle and Upper Devonian of the Baltic region (Gauja beds, Burtnecki, Upper Narova, Aruküla, Armata beds) and in sediments interpreted as freshwater deposits of Scotland (Nairn sandstone, Upper Ronsay series and Brindister flags) and Greenland (Tab. 1). *Asterolepis* juveniles occur in coastal marine waters (Lode, Latvia; Upeniece & Upenieks 1992), and by comparison with extant (or Pennsylvanian of the North American mid-continent) marine fish behavior (Gunter 1961) this is a further indication that *Asterolepis* lived in marine environments. The

Table 1. Distribution of some Red Hill I fishes in the Givetian/Frasnian.

Red Hill I	Eastern N America	E Greenland	Scotland	W Central Europe	Baltic NW Russia	Iran	Australia	S America
<i>Asterolepis</i>	●	○	○○○	●●	□□□□	●		●
<i>Machaeracanthus</i>	●●							
<i>Persacanthus</i>						●		
<i>Cheirolepis</i>	□		○	●●	□□□			
<i>Griphognathus</i>				●	□		●	
<i>Soederberghia</i>	○	○					○	
tristichopterids ¹	□		○	□	□		○○	

● = marine, □ = shallow marine, ○ = "freshwater", number of symbols = frequency of occurrence, ¹ = see text.

acanthodians, *Machaeracanthus* and *Persacanthus*, and the dipnoan *Griphognathus* are typical marine fishes (Campbell & Barwick 1988). The actinopterygian *Cheirolepis* appears to have been adapted to a marine environment, except for the occurrences in Scotland, which are interpreted as “freshwater” deposits (see Schultze 1999, p. 380). The occurrence of *Soederberghia* at Red Hill I is the only clear marine occurrence of the genus, even though Ahlberg et al. (2001) suggested the habitat of the genus as non-marine to shallow near-shore marine. The figured tristichopterid (there seem to be two different tristichopterids at Red Hill I) is very similar to *Eusthenopteron* and has been identified as *Eusthenopteron* by Reed (1979) and by Elliot & Johnson (1997) in biostratigraphic comparisons and by Schultze & Cloutier (1996) in paleoecological comparisons. In Table 1, the Red Hill I tristichopterid is recorded together with other tristichopterids to discuss the paleogeographic distribution of the group (see below).

The fishes at Red Hill I occur in a definitive marine environment as indicated by the invertebrate fauna. There is no indication that the fishes have been washed in; the bone beds are reworked zones closer to shore. Laterally the Red Hill I beds continue in limestones of marine origin. That habitat indicates marine adaptation of these fishes; their occurrences in putative freshwater deposits require an explanation if one accepts the sedimentological interpretations of the Scottish, Greenland and Australian localities. Either different species of these genera had different adaptations, or they could enter freshwater without too much difficulties as some marine fishes can today (in contrast: freshwater fishes except catadromous species cannot enter marine environments).

Comparison with other faunas

All the sponges (Rigby & Mehl 1994) despite their diversity are endemic to the Red Hill I Lagerstätte at species and in cases generic level. They are the last (*Cyathophycus*, *Protospongia*) or the first (*Actinodictya*, *Teganiella*) known occurrences of the genus. *Cyathophycella* is restricted during its whole temporal occurrences to the Roberts Mountains/Northern Simpson Park Range area of Nevada. *Actinodictya* is the only genus with species of similar age (Frasnian) in New York State. This connection to the eastern United States is supported by the occurrence of *Dictyospongia* in the Late Devonian rocks of New York State.

“Only one conulariid species, *Paraconularia recurvatus* Babcock & Feldman, 1986a, is represented, and it is endemic to the Red Hill I locality. *P. recurvatus* is the oldest species of the genus known from North America, and shows a morphology consistent with its inferred phylogenetic position as a form intermediate between Early to Middle Devonian species of *Conularia* and Mississippian species of *Paraconularia*. The close spac-

ing of rods is characteristic of a species in the presumed ancestral genus *Conularia*, whereas strongly reduced spines and, to a lesser extent, the recurvature of the rods, is characteristic of *Paraconularia* species. The only other known *Paraconularia* from the Devonian of North America are *P. chagriniensis* Babcock & Feldmann, 1986a, from the Upper Devonian of Ohio; *P. wellsvillia* Babcock & Feldmann, 1986a, from the Upper Devonian rocks of New York; and an undescribed species from the Devonian-Mississippian transition beds of South Dakota (Babcock & Feldmann 1986a). Worldwide, only two described species of *Paraconularia*, *P. africana* (Sharpe, 1856), and *P. ulrichana* (Clarke, 1913), are older than *P. recurvatus*. Both species are from Lower to Middle Devonian strata of the Malvinokaffric Realm in South America and southern Africa (Babcock 1993; Babcock et al. 1987). The genus *Paraconularia* has an Euramerican – Gondwanan distribution.” (Babcock).

The fishes at Red Hill I show a worldwide distribution on a generic level (Tab. 1) as can be expected from marine fishes. *Asterolepis* has its widest distribution around the Middle/Late Devonian boundary, as shown by Young (1981, 1993) and Janvier & Villarreal (2000). The distribution of *Asterolepis* coincides with the occurrences of the widely distributed antiarch *Bothriolepis*, for which Young (2003) suggested a dispersal through the sea. The acanthodian *Machaeracanthus* was widely distributed in the Early and early Middle Devonian. The actinopterygian *Cheirolepis* seems to be limited to the northern continents (Laurentia and Baltica at the time), whereas the dipnoans *Griphognathus* and *Soederberghia*, and the tristichopterid rhipidistians were cosmopolitan.

Young (1981, 1993, 2003) based migration pattern mainly on the “freshwater” occurrences of groups (xenacanth sharks, phyllolepid placoderms, large rhizodont crossopterygians and early tetrapod amphibians), which are not present in the Red Hill I fauna. He favors a migration of these groups from eastern Gondwana westwards. In contrast, I favor here marine occurrences of the Red Hill I taxa and like to argue that the marine adaptation of these genera (Tab. 1) gave them the freedom to move between areas. *Asterolepis* is known from Laurussia and northern Gondwana (South America); records from Australia (Denison 1978) are doubtful. The actinopterygian *Cheirolepis* is widely distributed in Laurussia, but not recorded from Gondwana. The lungfish *Griphognathus* is known from Laurussia and Australia from the earliest Frasnian; the Red Hill I occurrence is somewhat older as may be the occurrence in Bergisch Gladbach, Germany. *Soederberghia* co-occurs with early tetrapods in Australia, North America and Greenland. The occurrence in Red Hill I is the earliest and marine record of the taxon. These early occurrences of the two lungfish in Laurussia and later occurrences in Australia contradict Young’s proposed direction of migration. A special group of interest are the tristichopterids. Ahlberg & Johanson (1997) argued that

all primitive tristichopterids occur in Laurussia, a migration to Australia is postulated. Young (2008) countered that conclusion with establishing a new subfamily, Mandageriidae, for the advanced Australian tristichopterids. That excludes that endemic group from a migration pattern (Clement et al. 2009 suggested biogeographical barriers). The tristichopterid from Red Hill I is as old as the earliest Australian form and younger than the earliest *Eusthenopteron* records. In conclusion, it seems that there is no unidirectional migration, but an exchange between Laurussia and Gondwana (Young 2008).

The Red Hill I Lagerstätte was included in the comparison of the Escuminac Formation ichthyofauna with other late Givetian/early Frasnian ichthyofaunas by Schultze & Cloutier (1996), even though the Red Hill I ichthyofauna was not fully prepared and described at that time. The Red Hill I ichthyofauna appeared close to Russian and Baltic region ichthyofaunas on a generic level, and close to Scottish ichthyofaunas on family level in that analysis. The close connection to European localities is no problem for a marine fauna that could migrate along the continental margins. Red Hill I clusters with marine localities worldwide: Iran, Germany, Australia, northwest Russia, the Baltic region, Antarctica, and France. Gogo, Australia (Campbell & Barwick 1999), and Bergisch-Gladbach, Germany (Jux 1963; Schultze 1969; Jessen 1993), are marine localities of *Griphognathus*, and Koknese, Latvia (Gross 1956; Kuršs 1992; Lukševičs 2001), is a near-shore marine locality with *Griphognathus*. In contrast, the widely distributed localities of *Soederberghia* are interpreted as non-marine (Ahlberg et al. 2001) with the exception of Red Hill I, Nevada.

Schultze & Cloutier (1996) evaluated which fishes determined the clusters of localities and which indicated the depositional environments of the localities. The analysis resulted in a big cluster (assemblages II–V) of marine forms including *Griphognathus*, *Persacanthus* and a tristichopterid, *Eusthenopteron*. *Asterolepis* is part of assemblage I in Schultze & Cloutier (1996), the most widely distributed assemblage (in 24 of 38 localities). It occurs with other widely distributed genera having a marine preference, but also occurs in environments interpreted as freshwater deposits. Schultze & Cloutier (1996) concluded that there is no clear “freshwater” assemblage. Lelièvre (2004) reached the same conclusion for the Famennian using a different methodology. The interpretation of these fishes as marine is thus the most plausible one. All the “freshwater” occurrences, if correct, could represent migrations of these fishes into freshwater.

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