New approaches investigating freshwater palaeoecosystems

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Ecosystems are complex, self regulating interacting systems of communities and their abiotic environments (ELLENBERG 1973). But due to taphonomic and diagenetic processes only palaeocommunities are describable from the fossil record (BOY 1998). In this sense palaeoecosystems are complex interacting systems of palaeocommunities and abiotic environmental parameters. They show the following biotic features (SCHULZE & MOONEY 1993, BOY 1998): ecological structure, ecological function and biodiversity.
The ecological structure is determined by energy flow, what means that it is an interaction between all biotic components of the system (= synecology) and can be described through the trophic interactions (food chains, predator-prey interactions).
Because of time averaging, succession is the only detectable (palaeo-) ecological function (BOY 1998).
Palaeoecosystems analyses means therefore to investigate the biodiversity, trophic interaction and succession within and between palaeocommunities in relation to the abiotic environment.
An important precondition for the analyses of palaeoecosystems is the reconstruction of the palaeocommunity. To reveal the taphonomic processes (diagenesis, time averaging, biostratinomy,) is an important first step. To detect autochthon/parautochthon components within a taphocoenosis a new method is presented which is based on teeth replacement quotients of cyprinid fishes and allows to distinguish sediments from permanent water bodies with an autochthon fish community (limnic and fluvial sediments) from sediments of temporal water bodies (pedogenic sediments, pond and floodplain sediments) with parautochthon/allochthon fishes.
The investigation of 51 outcrops within the Upper Freshwater Molasse (Middle Miocene, Bavarian Molasse Basin) resulted in 21 localities with permanent water conditions, 27 with temporal water conditions (3 localities with uncertain conditions).

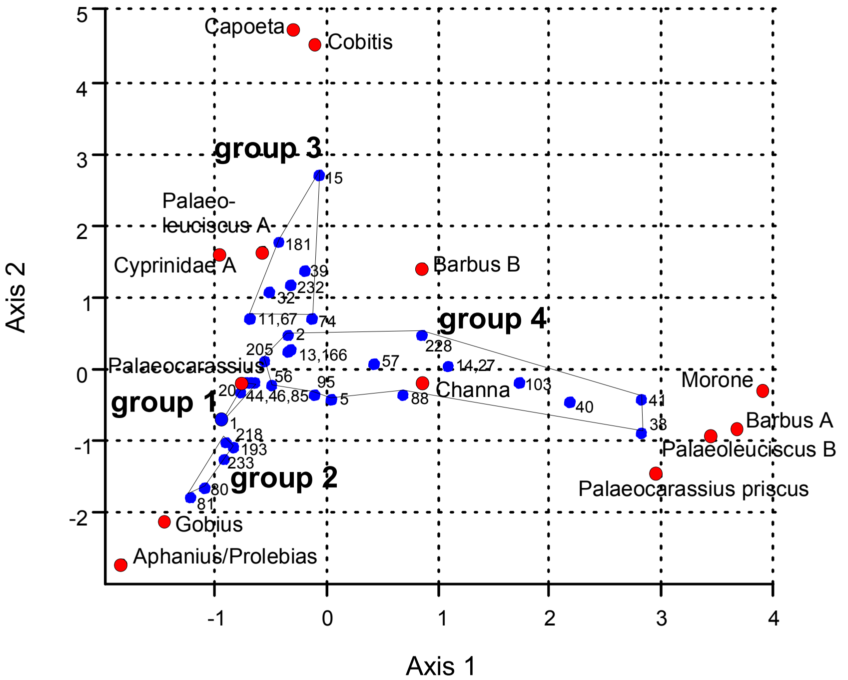

Fig. 1: Detrended Correspondence Analysis of 34 localities with permanent water conditions (Middle Miocene, Bavarian Upper Freshwater Molasse). (eigenvalues: axis 1: 0.5276, axis 2: 0.4611, axis 3: 0.4084) The numbers correspond to different localities (for explanation compare with Fig. 2)

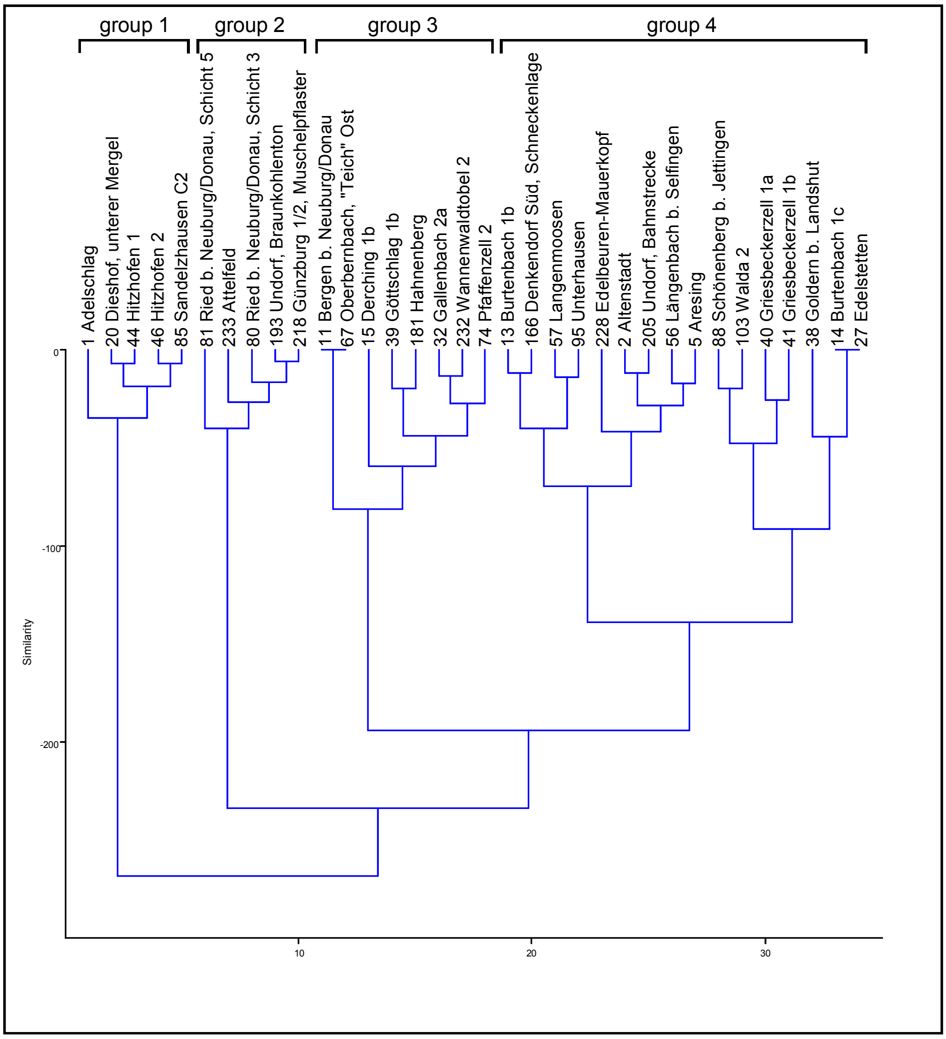

Fig. 2:Dendrogram of the hierarchical cluster analysis (Ward) of the same sample as in fig. 1.

The fish fauna of 34 localities with permanent water conditions are analysed statistically (Cluster analysis - Ward's method, detrended correspondence analysis). Both analysis show four clusters (group 1-4 in fig. 1 and 2). The clusters represent localities with a similar composition of the fish fauna. Fig. 3 gives a summery of the characteristic fishes, molluscs, aquatic and semi-aquatic floral elements, lithofacies and the proposed type of water body and foodweb of these four groups of localities.

Group 1 is characterized by a simple, detritus based (litoral) foodweb with detritivorous benthic organisms and zoobenthivorous fishes (fig. 4). Group 2 and 3 are characterized by a more complex, phytoplankton based (pelagic) foodweb with a filter feeding benthos – zoobenthivorous fish food chain and a zooplankton – zooplanktivorous fish food chain (fig. 4). Group 4 contains both types.

	group 1	group 2	group 3	group 4
characterising fishes	*Palaeocarassius* sp.	*Gobius* ssp., *Aphanius* sp. *Prolebias* sp.	*Capoeta*, *Cobitis*, *Palaeoleuciscus* sp. A, Cyprinidae A, *Barbus* sp. B	*Channa* ssp., *Barbus* sp. A+B, *Palaeocarassius priscus*, *Palaeoleuciscus* sp. B, *Morone* sp.
trophic groups (fishes)	zoobenthophag	zoobenthophag, zooplanktophag	zoobenthophag, zooplanktophag, detritivor, *aufwuchs* feeder	carnivor, omnivor, zoobenthophag
rheic groups (fishes)	stagnophil	stagnophil, euryök	euryök, rheophil	rheophil, euryök
characterising molluscs and their feeding mode	detritus feeder: (Planorbidae, Lymnaeidae)	detrititus feeder, filter feeder, grazer: (Planorbidae, Lymnaeidae, Bithynidae, Acroloxidae, Unionidae, Sphaeriidae)	filter feeder: (Bithynidae, Unionidae)	detritus feeder, filter feeder: (Planorbidae, Lymneaidae, Bithynidae, Unionidae, Sphaeriidae)
characterising aquatic and amphibic flora	*Nuphar, Stratiotes kaltennordheimensis, Chara molassica*	no record	*Potamogeton* ssp., *Lemna, Nymphea* ssp., *Brasenia, Hemitrapa, Scirpus, Ceratophyllum Nittelopsis meriani, Lychnothamnus, Chara* div. sp.	*Nymphea, Nuphar, Eoeuryale, Potamogeton, Epipremnum, Cladiocarya, Typha, Nittelopsis*
lithofacies	light/dark clays, marls, lignitic layers, +/- higher content on Markasit	light clays, marls	light/dark clays, marls, sandy marls, carbonate marls	fluvial sands (channel fill), sandy marls
type of water body	flat, less eutrophic riparian ponds under groundwater influence and without or minor temporal influence by the fluvial system	larger water bodies distantly from fluvial/riparian systems (lakes at the northern part of the basin)	slightly flowing stillwaters with temporal connection to the fluvial system (e.g. eutrophic oxbow lakes, oligo-mesotrophic spring water bodys)	rivers and flowing stillwaters with reedswamp vegetation
foodweb types	detritus based (littoral) food webs	phytoplankton based (pelagic) food webs	phytoplankton based (pelagic) food webs	phytoplankton and detritus based food webs

Fig. 3: Characteristic fishes, molluscs, aquatic and amphibic floral elements, lithofacies and the proposed type of water body and foodweb of the four groups of localities in Fig. 1 and Fig. 2.

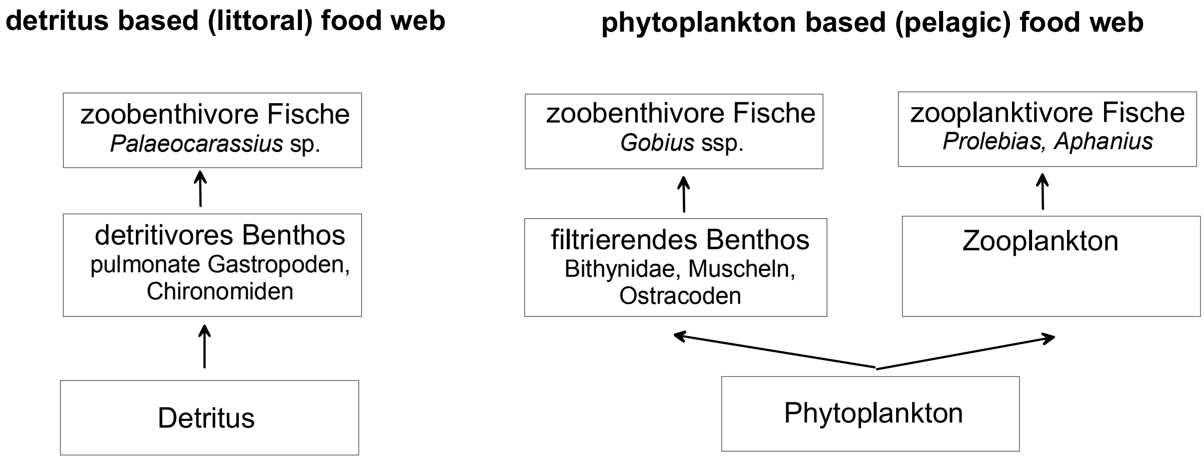

Fig. 4: Principal structure for the main types of food webs recorded in the palaeoecosystems of the Bavarian Upper Freshwater Molasse. Left detritus based (littoral) food web for localities of group 1 in Fig. 1 and Fig. 2. Right phytoplankton based (pelagic) food web for localities of group 2 and group 3 in Fig. 1 and Fig. 2.

One detritus based food web (Adelschlag see Fig. 1 and Fig. 2) and two phytoplankton based foodwebs (Gallenbach 2a, Derching 1b, see Fig. 1 and Fig. 2) are analysed more detailed.

Adelschlag

Most probably a flood or back swamp (lithology marls and lignitic marls) of large extension (some km). The fauna and flora is characterized (among others) by the zoobenthophagous fish *Palaeocarassius* and detritus feeding planorbid snails (both very abundant), divers ostracodes and few remains of the charophyte *Chara* sp. as the only floral element. The food web is based on detritus (high content of organic matter in the sediment) with the main food chain detritus → Planorbidae → *Palaeocarassius*. The features of the food web are given in fig. 8.

Gallenbach 2a

Small (50 – 100 m) eutrophic oxbow lake (lithology: dark bituminous clays – indicating high primary production) within a meandric river system. The fauna and flora is characterized (among others) by the zooplanktophagous fish *Palaeoleuciscus* (abundant), few *Chara* remains and divers and abundant aquatic makrophytes (four species of *Potamogeton, Lemna, Ceratophyllum*, two species of *Nymphea, Brasenia, Hemitrapa, Scirpus, Ranunculus*). The food web is based on phytoplankton with the main food chain phytoplankton → zooplankton → *Palaeoleuciscus*. The features of the food web are given in fig. 8.

Derching 1b

Oligo-/ mesotrophic water boby of unknown size (> 200 m) and type (probably a great lake with groundwater and/or spring influx). The lithology (sandy characean marl) and the faunal and floral composition are unique within the Molasse Basin. The fauna and flora is characterized (among others) by the zooplanktophagous fish *Palaeoleuciscus* (abundant), the zoobenthophagous and probably algae feeding fish *Capoeta*, divers ostracodes, abundant filter feeding snail (Bythinidae) and mass occurrence of Charophytes (up to six species). The food web is based on phytoplankton with the main food chain phytoplankton → zooplankton → *Palaeoleuciscus*. Other food chains based on algae (charophytes → *Capoeta*, aufwuchs → ostracodes → *Capoeta*, phytoplankton → *Bithynia* → *Capoeta*) are probably also important. A high number of omnivorous predators (*Chelydropsis, Trionyx, Channa, Mioproteus, Diplocynodon*) are remarkable.

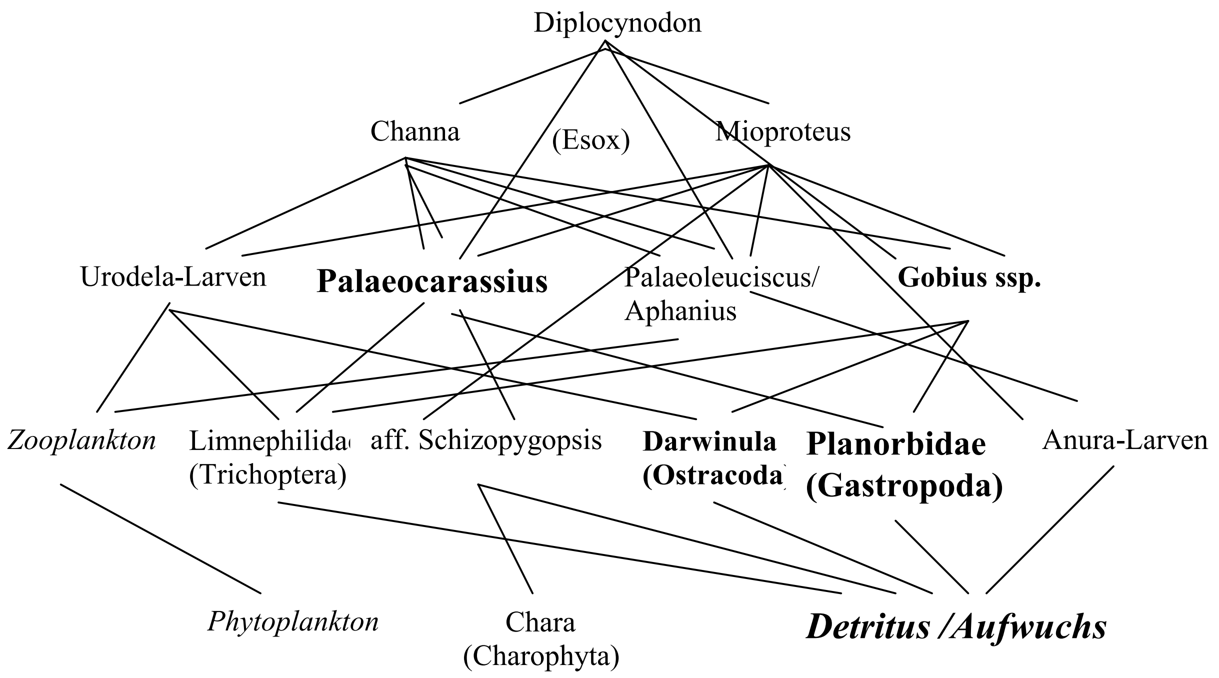

Fig. 5: Proposed aquatic food web of the locality Adelschlag.

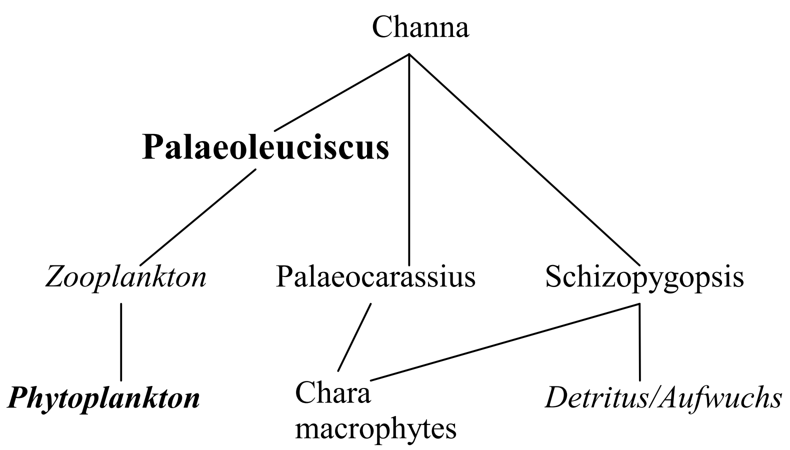

Fig. 6: Proposed aquatic food web of the locality Gallenbach 2a.

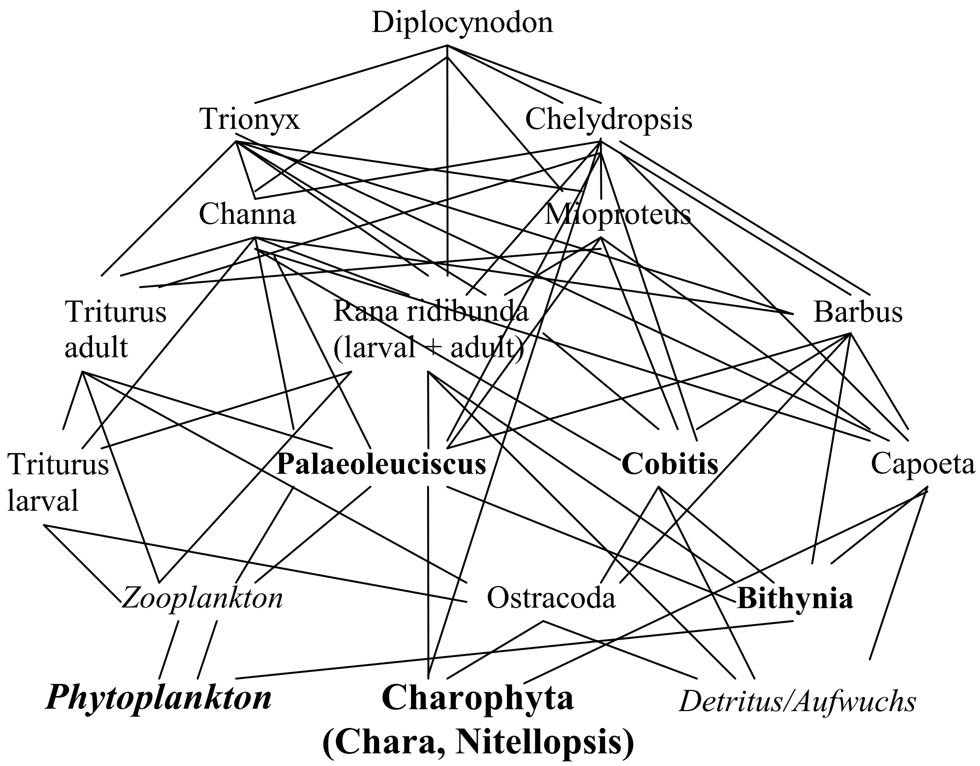

Fig. 7: Proposed aquatic food web of the locality Derching 1b.

	Adelschlag	Gallenbach 2a	Derching 1b
Number of trophic species	16	8	18
Number of chains	30	4	150
Maximum chain length	4	3	6
Main chain length	3.53	2.25	4.27
Number of links	33	8	48
productivity	middle	high	low
size	big	small	? big
stabiltity	high	middle	low

Fig. 8: Features of the food webs of Adelschlag, Gallenbach 2a, Derching 1b and the proposed productivity, size and stability of this palaeoecosystems.

The food-chain length is an important characteristic of ecological communities (PIMM & LAWTON 1977). The highest food-chain length is found in Derching, following by Adelschlag and Gallenbach (Fig. 8). Several hypothesis on the determination on food-chain size exist (productivity hypothesis, ecosystem-size hypothesis, productivity-space hypothesis, stability hypthesis; see POST et al. 2000). My investigations show no correlation between food-chain length and productivity or stability, but probably to the size of the palaeoecosystem (Fig. 8). This data would confirm the ecosystem-size hypothesis of COHEN & NEWMAN (1992) and HOLT (1993) and agree with the results of POST et al. (2000) on extant ecosystems.

Investigations on succession in freshwater palaeoecosystems are scares. Here I present the first results of a detailed analyse of a 5 m profile in a abandoned channel fill at the locality Pfaffenzell 2 – Weiler (fig. 9, 10).
The profile starts with dark, bituminous marls, rich in divers aquatic and semi-aquatic plants (*Woodwardia, Cladium, Trapa, Nymphea, Nuphar, Eoeuryale, Potamogeton, Stratiodes, Nittelopsis, Lychnothamnus*), the zoobenthophagous fish *Palaeocarassius*, the zooplanktophagous fish *Palaeoleuciscus* and the carnivorous fish *Channa*. This early stage of water body evolution can be characterized as eutrophic (fig. 9). The middle part of the profile contain light blue and grey marls with the charophytes *Nittelopsis* and *Lychnothamnus* as the only aquatic plant remains, the zooplanktophagous fish *Palaeoleuciscus* and the anadromous, carnivorous fish *Morone* (fig. 9). This stage of can be chartacterized as oligotropic. The upper part of the profile contain palaeosoils, indicating the end of the aquatic evolution.
The evolution of this water body from an eutrophic stage to an oligotrophic stage can be regarded as a regressive succession. This is in contrast with the observation in Holocene lakes in temperate regions, where an progressive succession (from oligotrophic to eutrophic) is the normal trend. As the reason for this regressive succession at Pfaffenzell a rise of the regional groundwater level during the middle part of the profile is supposed. Because the channal cut a potential aquifer (gravel of the Gallenbach Serie in fig. 9), oligotrophic groundwater influx has changed wetter climatic periods the trophic situation of the water body. On this base the channel fill can be classified as an spring pool.

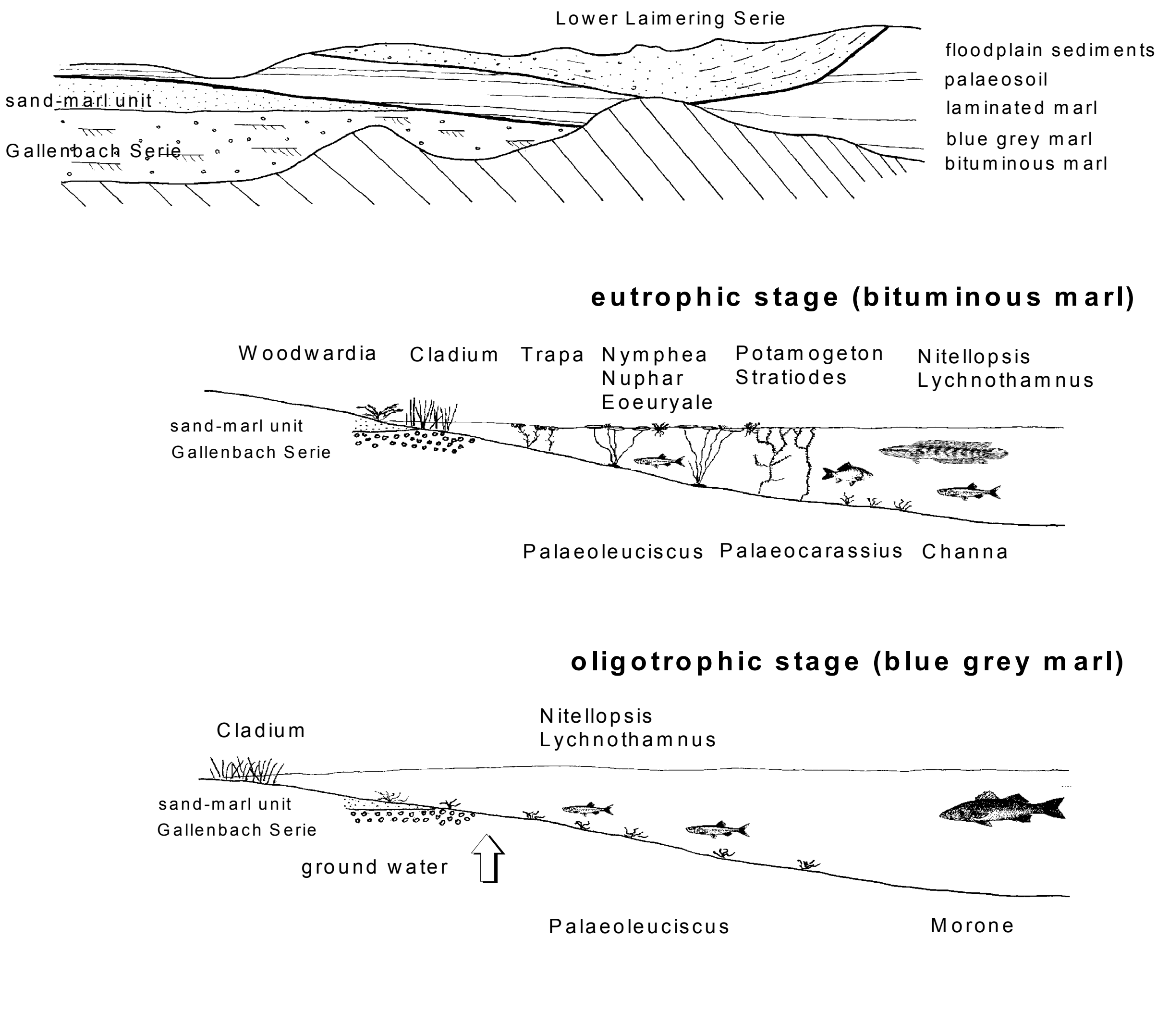

Fig. 9: Profile and reconstraction of the eutrophic and oligotrophic levels of the abandoned channel fill (spring pool) at Pfaffenzell 2 - Weiler

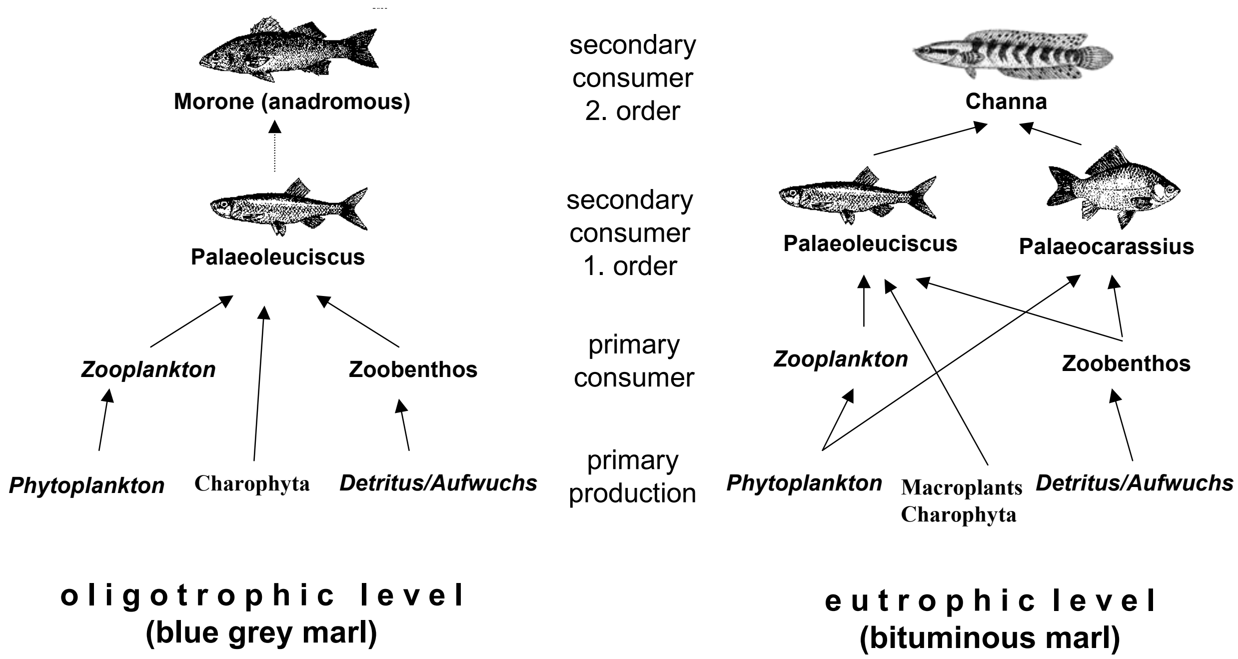

Fig. 10: Food webs of the oligotrophic and eutrophic level at the locality Pfaffenzell 2 – Weiler

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