Discussion of Košťák et al. (2021), Fossil evidence for vampire squid inhabiting oxygen-depleted ocean zones since at least the Oligocene.

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Košťák et al. (2021)[1] is important in presenting the first known Cenozoic fossil of a vampyromorph. Some modifications to the interpretations are needed, however. The first concerns inferring water depth habitat of non-benthic animals from fossils found in deep water sediments. The second concerns the water depth estimates for the La Voulte-sur-Rhône exceptionally preserved biota (La Voulte EPB), and the third, the implications for the model of post-Jurassic migration of Loligosepiids into deep water oxygen-depleted environments.

1. Košťák et al. (2021) concluded that '*Necroteuthis hungarica* inhabited bathyal environments with bottom-water anoxia and high primary productivity in salinity-stratified Central Paratethys basins.' Yet, inferring habitat in life from an isolated gladius, with no soft body preservation, and with unknown trajectory prior to incorporation in the sediment, is a brave task to attempt. Košťák et al. provide evidence for the existence of a surface low-salinity layer within which the coleoid would have been unable to survive, but offer no direct evidence for water depth habitat in life of *Necroteuthis*. The only constraint presented appears to be that it would have been greater than that of the base of the surface low salinity layer. What is the evidence for the range of corresponding water depths should be considered? Similarly, while evidence for oxygen-depleted bottom water at the sediment surface is presented, there is no evidence from the gladius itself that *Necroteuthis* lived in such bottom waters. A modern illustration of shallower water coleoids falling on death to a deep-sea sediment surface is provided by Hoving et al. (2017)[2]. Large lateral displacements caused by currents can probably also not be excluded.

2. The authors correctly summarise several observations from the La Voulte EPB arguing for dim-light deep water (>200 m) oxygen-deficient conditions and then state (p. 10) that 'coleoids in these environments still inhabited outer shelf close to the shelf/slope

margin during the Callovian, and did not yet expand to deeper bathyal environments' and that 'sedimentation took place on the outer shelf at ~200 m'. This may have been a misquotation of the reference cited (et al. 2014)[3], which states (p. 369), 'The cephalopods and other organisms (pycnogonids, asterids), have extant analogues that all live in deep-water niches always exceeding 200 m.' Indeed, the deep water benthic sponge and crinoid fauna was considered to have been resedimented into an even deeper water setting on a faulted slope. Non-benthic animals such as the coleoids may have lived at various water depths above the sediment surface at the La Voulte EPB depositional site, but observations of photophores typical of mesopelagic and bathypelagic coleoids (Rowe et al. 2023, p. 12)[4] suggest that at least some of them were adapted to the dysphotic bathyal environment above the sediment surface. The exquisite preservation of soft parts demonstrates an absence of scavenging prior to fossilisation, information that is entirely lacking in the case of *Necroteuthis*. In addition, Wilby et al. (1996, p. 849)[5] argued that the proportions of nektobenthic to nektonic forms present in the La Voulte EPB 'strongly suggests that the fauna was derived from near the seabed.' No coeval exceptionally preserved assemblages are known from locations further towards the basin centre, from which forms living at even greater water depths might be sampled, but absence of evidence in this case is clearly not evidence of absence.

The implications from points 1) and 2) above are that a bathyal niche (>200 m water depth) is likely to have been occupied by at least some vampyromorphs by at least Middle Jurassic times and that, while certainly plausible, a bathyal life habitat for the Oligocene *Necroteuthis* appears not to be demonstrated.

References

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