Trilobites in early Cambrian tidal flats and the landward expansion of the Cambrian Explosion

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We thank Paterson (2014) for calling our attention to the occurrence of the emuulid trilobite *Balcacocrania dailyi* in the lower Cambrian of Australia (Paterson et al., 2007), and for outlining further implications of our study (Mángano et al., 2014). We would like to expand on the nursery hypothesis and to outline some relevant methodological aspects.

The idea of trilobite nests goes back at least to Fenton and Fenton (1937), based on the occurrence of *Rusophycus jenningsi* in the lower Cambrian Lake Louise Formation of the Canadian Rocky Mountains. They described two closely associated deep bilobate structures that they attributed to the trilobite *Olenellus*, which occurs in the overlying St. Piran Formation, and interpreted the structures as nests, comparing them with traces produced by modern Limulus in coastal sediments. Eldredge (1970) explored the burrowing analogy between limulid nesting behavior, advancing the idea that trilobites may have forayed into very shallow water. Mángano and Buatois (2004) documented additional clusters (*Rusophycus*) in tidal-flat deposits of the lower Cambrian Pico de Halcón Member. These clusters were compared with those produced by limulid nesting behavior, advancing the idea that trilobites may have forayed into very shallow water. Mángano and Buatois (2004) documented additional clusters (*R. lefevikssonii*) in tidal-flat deposits of the lower to middle Cambrian Campanario Formation. These authors advanced four hypotheses that may explain the presence of trilobite trace fossils in intertidal areas: the trilobite nursery, trilobite pirouette, hunting burrow, and microbial garden hypotheses. In summary, the idea that trilobites forayed into the intertidal zone for reproductive behavior has a relatively long history. Though all these earlier studies emphasized ichnologic data, together with the search for modern analogs, subsequent work by Paterson et al. (2007) arrived at similar conclusions regarding comparisons with limulids from the perspective of body fossils, albeit being apparently unaware of previous ichnologic work.

From a methodologic standpoint, multiple working hypotheses are recommended. The four scenarios outlined should be tested empirically. For example, the nursery hypothesis would be supported by clusters of deep *Rusophycus* rather than isolated specimens. Also, in deposits where trilobites used intertidal flats only as nurseries, we would expect a high density of traces on a relatively low number of bedding planes, accounting for the sporadic timing of trilobite incursions. Neither clusters nor this distribution of bioturbation intensities are apparent in the Rome Formation. In deposits where trilobites used intertidal flats as feeding grounds, we would expect a higher frequency of excursions and many or most beds within the intertidal realm to be bioturbated by trilobites. This is the case in the Rome deposits we have analyzed so far. Paterson underscored the intergradations between *Rusophycus* and *Cruziana* by stating that “[a]lthough these types of traces could represent foraging (*Cruziana*) and resting/feeding (*Rusophycus*) (Seilacher, 2007), they may be a record of nest site searching and excavation.” We find the last part of this statement problematic. These intergradations do not represent evidence of nesting behavior. They are so common that adopting this line of reasoning would lead to reinterpretating a large proportion of records of these ichnogenera in shallow-marine settings as nesting sites. In the absence of morphologic evidence supporting the nursery hypothesis in the Rome Formation, we find no empirical grounds to favor the idea of incursions for reproductive purposes, instead favoring feeding behavior.

The potential reasons for trilobite incursions in intertidal areas inevitably involve a higher degree of interpretation than simple documentation (i.e., sedimentologic evidence of tidal flats and ichnologic evidence of trilobite activity). We agree with Paterson that the occurrence of body or trace fossils of trilobites in intertidal deposits is important in itself, because it requires that the assumption that all trilobites were restricted to subtidal settings be revised. More speculatively, it shows that trilobites would have altered their environment by disturbing the ubiquitous microbial mats. Reduced mat cover and increased reworking of sediment may, in turn, have raised the turbidity of overlying water, increased penetration of oxygen into the substrate, and heightened the abundance and penetration of the substrate by a cohort of organisms.

REFERENCES CITED


