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Observations of tadpole nest-like structures in four temporary pools in northern and central Italy

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The interactions between anuran tadpoles and the sedimentary substrates in which they complete metamorphosis remain poorly understood. Likewise, reports of networks of inverted cup-shaped depressions produced by tadpoles within soft sediments, commonly referred to as honeycomb-like structures or tadpole nests (Cameron and Estes, 1971), are scarce. Similar surface geometries have been described from a variety of sedimentary and biological contexts, including the deep-sea trace fossil classified in the ichnogenus[2] *Paleodictyon*. However, these similarities are purely morphological and do not imply comparable biological processes. The earliest records of tadpole nests date back to work by the geologist Edward Hitchcock, who in 1856 gave a presentation entitled Mud-nests of the tadpole: recent and fossil as recorded by Lovering (1857). Sacco (1899) discussed Hitchcock's findings and concluded that they should not be considered *Paleodictyon*, but De Alessandri (1900), who documented indentations produced by *Bufo vulgaris* tadpoles near Ravanasco Stream in northern Italy, once again considered the similarities. More recent reports of such structures have come from non-Italian terrestrial sedimentary environments (Maher, 1962; Alarcos, 2018; Fuentes and Atance, 2020).

Anuran oviposition sites located along the margins of waterbodies are generally regarded as an adaptive strategy that provides larvae with environmental conditions favourable for successful metamorphosis (Fischer, 2023). The formation of nests by tadpoles has primarily been interpreted as a behavioural response associated with feeding and thermoregulation in temporary waterbodies, such as puddles (Annibale et al., 2019). In the absence of external disturbances, these microhabitats do not dry out until metamorphosis is completed (Fuentes and Atance, 2020). Puddles may also reduce predation risk to tadpoles because predatory fish cannot access them and they do not last long enough for the development of odonate larvae (Stav et al., 2007).

Temperature is one of the principal environmental factors regulating tadpole growth and development (Reading, 2010; Dastansara et al., 2017). Tadpoles confined to shallow waterbodies undergoing rapid evaporation, where water temperatures can rise quickly, frequently display behaviours such as burrowing and the excavation of shallow depressions (Richter et al., 2008). Construction of such microhabitats may represent an adaptive response that optimises local environmental conditions and maximises developmental success within the limited duration of the hydroperiod (Drakulić et al., 2017). Here, I report observations of tadpole nests recorded between 2019 and 2024 at four sites in Italy, occupied by larvae belonging to the genera *Bufotes* and *Bufo*.

Three of the observations involved *Bufotes viridis* (Laurenti, 1768) tadpoles inhabiting temporary sedimentary pools undergoing rapid desiccation. The fourth consisted of networks of subcircular depressions produced by *Bufo bufo* (Linnaeus, 1758) tadpoles within an unusual algal substrate that had developed inside a watering hole for livestock. The aims of this study are to document these observations for Italy, to report for the first time the occurrence of analogous nest-like structures in an algal substrate, describe their morphological characteristics, and briefly discuss possible interpretations of their formation, without assigning a definitive functional significance to these structures.

Material and Methods

Study sites. During a seven-year period, while conducting field surveys primarily aimed at faunistic and ecological research, tadpole nests were fortuitously discovered at four localities in northern and central Italy. The study sites are described below.

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[2] An ichnogenus is a genus-level classification in palaeontology to group trace fossils. This term does not categorise the organism but the marks it left behind (e.g., dinosaur footprints, worm burrows, bite marks).

San Pietro.—The Fiora River, Ischia di Castro, Viterbo Province (42.5275°N, 11.6022°E) flows through a well-preserved natural landscape. The San Pietro site is located within a deep gorge carved by the river and falls within the Sistema fluviale Fiora-Olpeta Special Area of Conservation. On 6 June 2019, three puddles containing honeycomb-like structures associated with the breeding activity of *Bufotes viridis* were identified on the river's sandstone banks.

Le Piane.—This site is located in Tarquinia, Viterbo Province (42.2836°N, 11.7916°E) within the Marta River floodplain and is characterized by alluvial and colluvial deposits consisting of clays, silty clays, and grey sands. The puddle was situated along the margin of an unpaved rural road within a predominantly agricultural landscape. On 2 May 2025, a completely desiccated tadpole nest was discovered, which contained the desiccated remains of *B. viridis* tadpoles.

Polecra.—At this site in Lonato del Garda, Brescia Province (45.4394°N, 10.4974°E), tadpole nests produced by *B. viridis* were documented on 30 May 2021. The structures occurred within a shallow clay-bottomed temporary puddle that had formed following approximately one month of frequent and intense rainfall. The puddle was located alongside a rural track adjacent to cultivated fields.

Fontanile del Vallone.—On 6 June 2024, a nest-like structure comparable to tadpole nests was documented within an algal substrate in the Collarmele Valley, L'Aquila Province (42.0802°N, 13.6479°E). The observation was made in a livestock watering facility consisting of three interconnected troughs located near the boundary of the Sirente Velino Regional Park, within the Sirente Velino Special Protection Area. The site lies within a valley bordered to the west by the slopes of the Sirente Mountains.

Morphometric data. For each study site, the diameters of ten cup-shaped depressions (Fig. 1) belonging to the same nest structure and the total body length (snout-to-tail tip) of ten tadpoles occupying that structure were measured. Morphometric data were obtained indirectly from photographs taken in the field. Measurements were performed retrospectively using Snake Measurement software, version 1.0 (Tsai et al., 2018), by calibrating image scale against reference objects visible in the photographs or, when these were unavailable, against a selected reference tadpole. Because this procedure is subject to potential sources of error – including camera angle, perspective, lens distortion, and the accuracy of photographic scaling – all measurements should be regarded as approximate.

The relationships between the continuous variables were evaluated using Pearson's correlation coefficient and simple linear regression models. For each model, the coefficient of determination (R^2) and the corresponding significance level were calculated. Statistical analyses were performed separately for each study site using RStudio v2025.09.1, adopting a significance threshold of $p < 0.05$.

Results

All observations were made on nest structures that had already been established. At the San Pietro site, several areas with depressions were distributed across an approximately 225 m^2-section of the riverbank (Fig. 2), whereas only a single honeycomb-like structure was recorded at each of the remaining sites. Occupancy varied markedly among the structures: some were almost completely devoid of *B. viridis* tadpoles, whereas others contained large numbers. One nest was completely desiccated and, in several cells, contained the desiccated remains of dead tadpoles.

Field observations indicated that individual cup-shaped depressions could be occupied either by a single tadpole or by several. Tadpoles moved continuously between adjacent cells, regardless of whether the destination cell was vacant or already occupied. When a tadpole entered an occupied cell, the resident individual frequently moved to a neighbouring depression, generating a sequential displacement of larvae throughout the structure. During grazing activities, or while generating the propulsive force required to move between adjacent depressions, tadpoles repeatedly oscillated their tails around their centre of mass, resuspending sand and silt particles from the substrate (Wassersug, 2000). A video documenting this behaviour is available at the linked website.

The occurrence of a honeycomb-like structure within a non-sedimentary algal substrate at Fontanile del Vallone associated with *B. bufo* tadpoles represents an unusual observation and, to the best of my knowledge, has not previously been reported. Only a single such structure was seen, in the uppermost trough of the watering facility. This was also the only trough where an adult female *Triturus carnifex* was recorded.

Given the intense and continuous movements of the tadpoles, together with the possibility that the observed larval assemblages originated from multiple oviposition events, no relationship between tadpole body size and the dimensions of the cup-shaped depressions was expected.

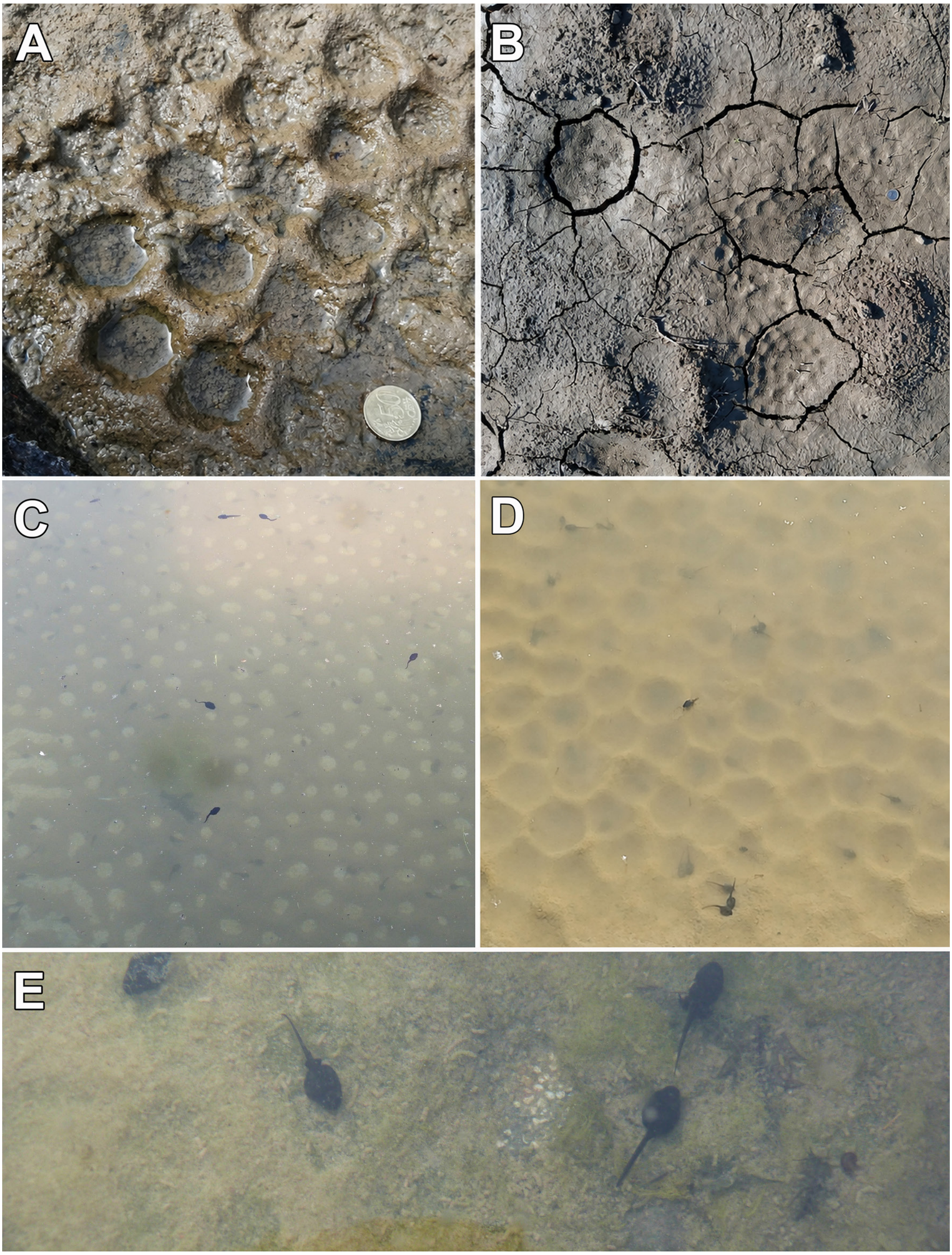

Figure 1. Representative images of the cup-shaped depressions found associated with tadpoles in northern and central Italy. (A) Close-up of a dried section in San Pietro (Fiora River). (B) Overview of a recently dried section in Le Piane. (C) Depressions with algal growth in a puddle Fontanile del Vallone. (D) Depressions in a still-active puddle in Polecra. (E) Close-up of tadpoles on a bed filamentous green alga (Zygnemataceae) at Fontanile del Vallone.

Figure 2. Riverbank puddles at San Pietro, Fiora River, with depressions at stages of drying, some with and some without larvae.

Consistent with this prediction, neither Pearson's correlation analyses nor simple linear regression models revealed statistically significant relationships between tadpole total length and depression diameter at any of the study sites (Table 1; Fig. 3).

Discussion

The observations presented here document the occurrence of tadpole nests in central and northern Italy and reveal an unusual and rarely reported spatial organization of substrates, which appears to be previously undocumented in the case of algal formations. These structures were consistently associated with the presence and activity of tadpoles at the four study sites, on different substrates, and across different years. In addition to the mechanical effects generated by body movements during grazing activity and the propulsive forces required for movement between adjacent depressions, several other factors may contribute to the development of these structures. These include

Table 1. Descriptive statistics and linear regression analysis between mean larval length and mean diameter of cup-shaped depressions (⌀) across the four sampled sites. Measurements are given to the nearest 0.1 mm ± standard deviation. The other columns present additional statistical data, including the Pearson correlation coefficient (*r*), the coefficient of determination (R^2), the slope of the regression line (β), the standard error (*SE*), intercept (I), and *p*-value. All analyses returned non-significant p-values. The last column provides the corresponding Gosner developmental stages of the observed tadpoles, where M indicates the presence of multiple stages.

Site	Length	⌀	*r*	R^2	β	*SE*	I	*p*	Gosner
San Pietro - Fiume Fiora	17.0 ± 2.3	34.7 ± 2.7	0.124	0.015	0.142	0.402	32.325	0.733	39–42
Le Piane	13.3 ± 4.9	26.9 ± 3.7	0.086	0.007	0.063	0.261	26.085	0.814	26–30
La Polecra	16.0 ± 0.9	22.4 ± 2.7	0.371	0.138	1.161	1.026	3.740	0.291	26–27
Il Vallone	15.2 ± 1.6	13.7 ± 3.0	-0.095	0.009	-0.178	0.658	16.416	0.793	M

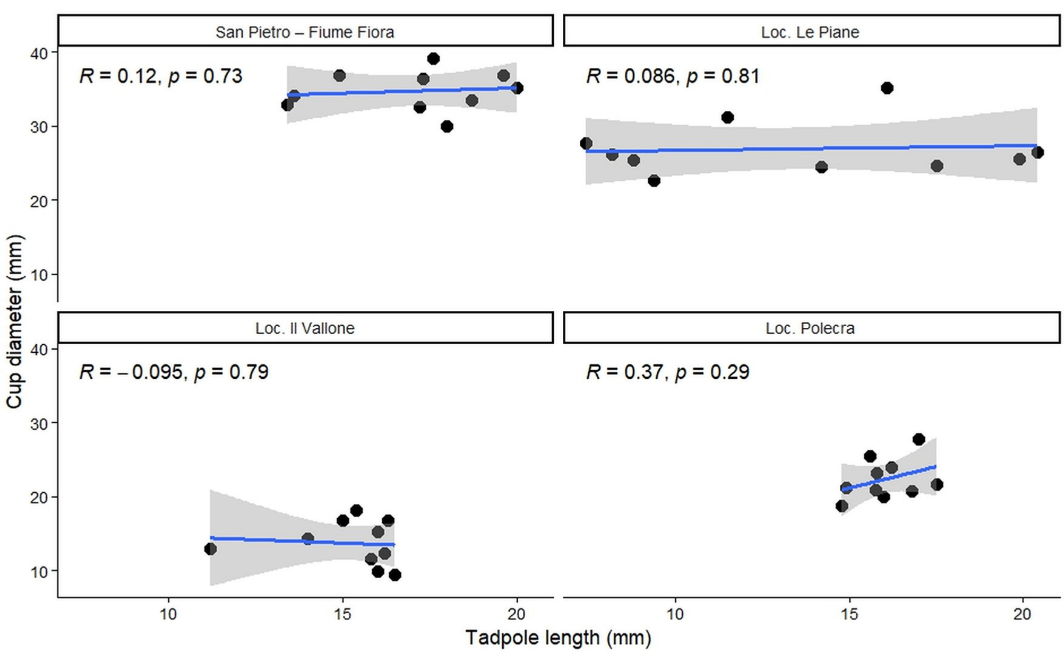

Figure 3. Relationships between tadpole length and the diameter of cup-shaped depressions across the four sampling sites. Solid lines represent linear regression models; Pearson's correlation coefficients (*r*) and corresponding *p*-values are reported for each site. The sampling sites are arranged in clockwise order.

physical and chemical processes affecting the substrate and surrounding water, site-specific sedimentological characteristics, or the influence of other unobserved biotic processes. The observations collected in this study do not allow discrimination among these alternative explanations.

Similarly, potential behavioural advantages associated with tadpole nest formation, including protection from predators, reduction of thermal stress, optimization of spatial use, possible enhancement of predator avoidance, or improved grazing efficiency, should currently be regarded as hypotheses requiring experimental validation.

The observation of a structure comparable to sedimentary tadpole nests developing within algal mats suggests that similar geometric patterns may arise in different types of substrates. However, it remains impossible to determine whether the underlying formative processes are homologous. Furthermore, no significant relationship between larval body length and the diameter of cup-shaped depressions was detected at any of the investigated sites. The formation and dimensions of these depressions may instead result from the cumulative effects of multiple processes, including the number of individuals involved in their formation, the frequency and intensity of movements between adjacent cells, grazing activity, duration of aquatic exposure, and substrate characteristics.

Biomechanical and biochemical approaches may provide valuable insights into the processes responsible for the formation of these structures under specific geomorphological conditions. In addition, further investigations into the quality and availability of trophic resources, such as planktonic communities, within the substrates where these structures develop may help clarify the role of grazing activity in their formation.

The available data currently do not explain why nest-building behaviour in bufonid tadpoles is not regularly observed, nor why it appears to be restricted to certain taxa. These findings highlight the need for further research into the mechanical, ecological, and behavioural factors underlying the formation of these structures, which remain comparatively poorly understood.

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