

Reproductive cycles of the European amphibians: A brief history of studies on the role of exogenous and endogenous factors

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Abstract. The European amphibians show seasonal reproductive cycles typical for each species. This behaviour allows that mating, egg-laying and larval development occurs when environmental conditions are most favourable. In addition to exogenous factors (mainly temperature), also endogenous mechanisms (hormonal in nature) play a crucial role in the periodicity of the sexual activity. In this context, we wish to recall the researches of Mario Galgano in clarifying the dynamics of the reproductive cycles on the basis of both external and internal constraints. Galgano described the whole process of gametogenesis in several anurans and urodeles, both under natural and experimental conditions. In addition, from the observations of various species Galgano recognized two different types of gametogenesis (really discontinuous and potentially continuous) according to the prevalence of endogenous rhythms or environmental conditions, respectively.

Mode and time of reproduction in amphibians depends strictly on physiological and morphological responses of these vertebrates to the environment, on the basis of endogenous and exogenous mechanisms. The result is an extraordinary variety of breeding patterns reflecting a compromise among many selective pressures (Duellman and Trueb, 1986).

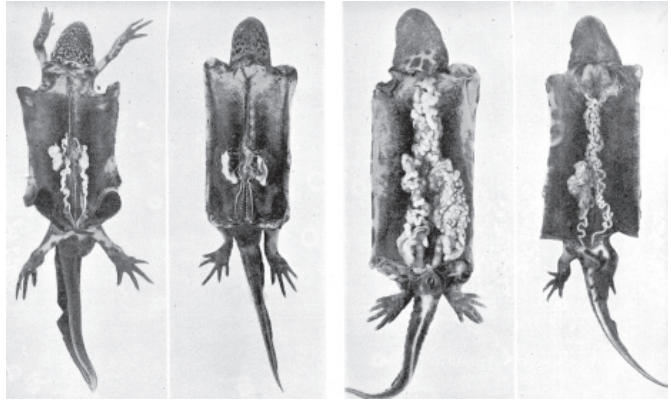
All amphibians of temperate areas, therefore including Europe, show a seasonal reproductive activity that ensures that mating, egg-laying and larval development can take place at those times of the year when environmental conditions are most favourable (Halliday, 1990; Griffiths, 1996). As a rule, the reproductive season is initiated by rising temperatures and spring rains and in some cases extends into the summer. The autumn, usually characterized by an equally suitable climate (at least in the Mediterranean regions) is less used by the amphibians for reproduction. Possibly, this depends on selective and adaptive processes related to the short duration of appropriate conditions, followed by a rapid decrease of temperatures and considerable difficulties for the larvae to complete their development before the winter.

However, the tight correlation between reproductive pattern and climatic parameters is underlined by the comparison of populations of the same species distributed in different areas, for example populations on mainland and islands, or on plains and mountains. Accordingly, the sexual activity is

early or late. The only European amphibians which do not display a clear cyclic pattern of breeding are those that live permanently in caves (*Proteus anguinus*; Durand & Bouillon, 1964), as these environments fluctuate much less in temperature and other physical parameters than surface habitats. In amphibians, reproduction uses up a lot of energy resources (mainly stored in the form of fat bodies) and both sexes must be ready as soon as environmental conditions become favourable. For this reason, all amphibians of temperate regions go through an annual cycle of physiological changes which produces growth and regression of gonads and hormonal changes related to the reproductive activity. At present, it is well known that the mechanisms of hormonal controls are subject to some genetic limitations and their integration produces certain reproductive patterns as a reaction to environmental variables and further constraints imposed by the organism's microhabitat and its species-specific characteristics (Duellman and Trueb, 1986; Houck and Woodley, 1995).

In this respect, we wish to recall the researches of Mario Galgano (1907-1985; Fig. 1) in clarifying the role of exogenous (climatic) and endogenous (mainly hormonal) factors on the reproductive cycles of the European amphibians, both anurans and urodeles. M. Galgano has been one of the most active researchers of the 20th century in the field of amphibian reproduction. On the basis of his wide knowledge of the international literature on this subject, he produced about 80 papers devoted to amphibian caryology, sexual determination

Figure 4. Male (A-B) and female sexual apparatus (C-D) of *T. carnifex* collected in different seasons. A and C: animals in spring reproductive phase, B and D animals in reproductive stasis and gonadic regression in late summer (from the original paper of Galgano, 1944, Tab.II).



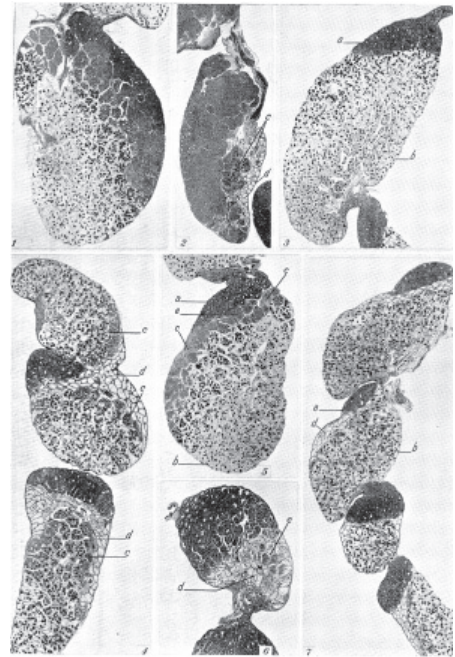
blocked by inappropriate environmental conditions, but can start again when the climatic conditions become better. In these cases we have a potentially continuous gametogenesis (Galgano, 1952 a,b).

The dynamics of reproductive cycles in Amphibia is also under endocrine control, as pointed out by further Galgano studies. From 1940 on, the author focused his attention on the effects of hormonal applications to amphibians at different phases of their reproductive cycles and maintained in experimental conditions (Galgano, 1942a, Galgano and Lanza, 1951). Besides the tight correlation between hypophysis and gonadic activity, the author noticed hormonal control also on secondary sexual characters (Galgano, 1940, 1942b), for example the mating livery (fig. 7). In particular, he demonstrated that the gametogenetic stasis and the regression of the secondary sexual characters depend upon a scarce release of gonadotrophins by the hypophysis. Concerning the production of the latter, this may depend on external factors -as in the case of the potentially continuous cycles- or on strictly endogenous mechanisms, as typical in the really discontinuous cycles. The identification of these two different types of mechanisms is one of the most important results of Galgano's research, and still today these criteria are fundamental for all studies on the reproductive biology of the amphibians (for a review of Galgano's results and a wide discussion on the sexual cycles of the European amphibians see Lanza, 1951).

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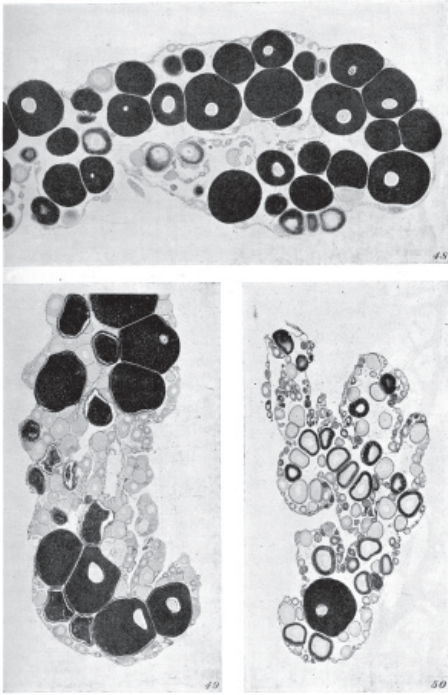
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Figure 5. Sections of testes of *T. carnifex* collected in different seasons (explanations in the original paper of Galgano, 1947, Tab. I).



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Figure 6. Sections of ovaries of *T. carnifex* collected in different seasons (explanations in the original paper of Galgano, 1947, Tab. V).



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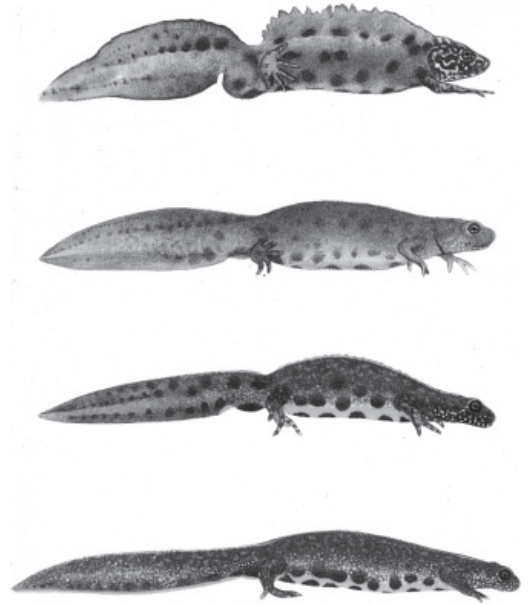
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Figure 7. Seasonal variations of the secondary sexual characters in *T. carnifex* (from the original paper of Galgano, 1944, Tab.I).



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