

RESEARCH REPORT

Teratological changes on the prosoma of *Eratigena atrica* spiders caused by alternating temperatures**T Napiórkowska, J Templin***Department of Invertebrate Zoology, Faculty of Biology and Environmental Protection, Nicolaus Copernicus University, Lwowska1, 87-100 Toruń, Poland**Accepted November 14, 2017***Abstract**

Environmental temperature has a tremendous impact on many areas of spiders' lifestyle. It can also be a strong teratogen. The study presents the results of teratological research involving embryos of *Eratigena atrica* spiders. It was aimed at demonstrating a relationship between the temperature of embryo incubation and the mortality of embryos as well as the number of individuals with body deformities. The experiment was based on the application of alternating temperatures as a teratogenic agent. *E. atrica* embryos were exposed to temperatures of 14 and 32 °C changed every 12 h for the first 10 days of their development. We observed that these alternating temperatures significantly influenced embryo mortality and the number of body deformities. Embryo mortality was high and the experimental group contained 40 individuals with different anomalies of the prosoma: oligomely, schistomely, heterosymely, symely and bicephaly. Four individuals were affected by so-called complex anomalies, (combination of several defects). Complex anomalies of appendages on the prosoma were recorded for the first time in the history of our research. Since each case was different, we analyzed and described each of the spiders separately.

Key Words: alternating temperatures; complex anomalies; malformations; spiders**Introduction**

In arthropods collected in the natural environment deformities are reported frequently. In the majority of cases these anomalies affect external structures (particularly appendages on certain body segments) and the exoskeleton (Shelton *et al.*, 1981; Spanò *et al.*, 2003; Małol and Łaydanowicz, 2006; Asiain and Márquez, 2009; Gregati and Negreiros-Fransozo, 2009; Fernandes *et al.*, 2010). More complicated cases include conjoined twins and *duplicitas posterior*, all observed in juveniles obtained from embryos collected in the wild and transferred to the laboratory (Jara and Palacios, 2001; Rudolph and Martinez, 2008; Janssen, 2013). It is impossible to identify a factor/factors responsible for malformations in individuals found in nature; the most likely causes are therefore investigated (Čurčić *et al.*, 1983; Eeva and Penttinen, 2009). However, deformities can also be induced in strictly controlled laboratory conditions by disturbing embryogenesis

using a certain teratologic factor, e.g., humidity (Buczek, 2000) or chemical compounds (Itow and Sekiguchi, 1979, 1980; Buczek, 1992). Temperature is yet another powerful teratogen. Embryo incubation at temperatures significantly different from the species optimum may lead to a number of developmental deformities (Juberthie, 1962, 1963a, b).

Among arthropods these are arachnids, including spiders, that are often used in teratological studies. Similarly to other arthropods, spiders are poikilotherms. However, they are commonly referred to as ectotherms due to the fact that their body temperature is determined mainly by passive heat exchange with the surroundings (Punzo, 2007). Temperature has a huge impact on many areas of spiders' lifestyle including mating behavior (Davis, 1989), escape speed (Cobb, 1994), food intake and growth (Aitchison, 1981), copulation duration (Costa and Sotelo, 1984), net casting (Barghusen *et al.*, 1997), nest site choice (Hanna and Cobb, 2006), and intervals between egg deposition (Downes, 1988). According to Li (1995, 2002) Darymple (2005) Hanna and Cobb (2006), temperature is the main factor influencing egg hatching and the duration of embryogenesis and post-embryogenesis as well as the survival of juvenile stages. In the optimum temperature embryogenesis is undisturbed

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and embryo mortality is low. An increase in incubation temperature usually accelerates embryogenesis, while a decrease delays this process (Pulz, 1987). The studies of Jacuński (1969, 1971) and Mikulska and Jacuński (1970, 1971) demonstrate that the application of temperature higher than the thermal optimum (supra-optimal) (32 °C) of *Eratigena atrica* (previously known as *Tegenaria atrica*) may impair their morphogenetic processes, leading to body deformities. In subsequent experiments the exposure of embryos to temperature changed at regular intervals (lower and higher than the optimum) led to a higher number of individuals with anomalies and more complex changes in their prosoma and opisthosoma than when a single thermal shock was applied. These alternating temperatures (14 and 32 °C) used as a teratogenic agent were responsible for oligomely, heterosymely, polymely, schistomely, symely, and bicephaly in spiders (Jacuński, 1984; Jacuński and Templin, 2003; Jacuński *et al.*, 2004; Templin *et al.*, 2009, 2009-2010; Napiórkowska *et al.*, 2010a, b, 2016; Napiórkowska and Templin, 2013). In addition, in some cases the structure of internal organs is investigated (especially the central nervous system) to assess changes corresponding to particular deformities (Jacuński *et al.*, 2002a, b, c, 2005; Napiórkowska *et al.*, 2010a, b, 2013, 2015).

We put forward a hypothesis that the application of alternating temperatures (14 and 32 °C) would significantly affect the mortality of embryos and number of deformities in *Eratigena atrica*. The experiment was aimed primarily at evaluating the effect of thermal conditions on spider embryonic development. Another objective was to present several examples of developmental deformities in spiders in order to demonstrate changes in their morphology caused by temperature used as a teratogen. Morphological changes analyzed in this study were identified for the first time in the history of teratology.

Materials and Methods

The study involved embryos of *Eratigena atrica* (Agelenidae). 43 sexually mature females and 17 males were collected during one breeding season in August 2015 near the towns of Chelmża and Toruń (Poland) and transported to the laboratory, where each spider was put into a separate glass container with a capacity of 250 cm³. Spiders were kept in a dark room at the temperature of 21 - 23 °C and relative humidity of 70 % and fed twice a week larvae of *Tenebrio molitor* Linnaeus. Water was

provided regularly. Three weeks after the culture was established, a male was introduced into the container with a female ready for fertilization. The procedure was repeated after two weeks. First cocoons were laid at the end of November. Embryos were immediately removed from the containers, then counted and divided into two groups: the control group, maintained at the temperature of 22 °C and the humidity of 70 %, in conditions optimal for the embryonic development of this spider species (Jacuński and Wiśniewski, 1997). The experimental group was exposed to temperatures of 14 and 32 °C (both significantly deviating from the optimum) applied alternately every 12 h. This method was applied for the first time by Jacuński (1984). The procedure continued for ten days, until the first metameres of the prosoma appeared on the germ band. Subsequently, all experimental embryos were incubated under the same conditions as the control ones. Hatching took place approximately 20 days after the eggs were laid. All control and experimental larvae were evaluated for developmental deformities.

A relationship between incubation temperature and embryo mortality was tested using χ^2 test for a contingency table. The same test was used for the number of anomalies, with Yates correction for small abundances.

Results

During one breeding season we obtained approx. 1,200 embryos, half of which constituted the control group. Individuals from this group were not affected by any developmental abnormalities. Embryo mortality was 5 % in the control group and about 30 % in the experimental group, due to the incubation temperature ($\chi^2 = 129.9$, $df = 1$, $p < 0.0001$). 40 individuals had leg anomalies. The number of teratogenically modified individuals was related to alternating temperatures ($\chi^2 = 54.1$, $df = 1$, $p < 0.0001$). The highest number of larvae were affected by oligomely, *i.e.*, they had a reduced number of legs on the prosoma. Teratological material also contained individuals with schistomely (bifurcation) of walking legs, heterosymely (fusion of legs lying next to each other on the same side of the prosoma), and symely (fusion of legs of the same pair, lying opposite each other on the prosoma). In addition, one individual was affected by bicephaly (presence of two heads) and four others, by complex anomalies, *i.e.*, a combination of at least two deformities (Table 1). Since the majority of these

Table 1 Kinds and frequency of anomalies in the prosoma in *Eratigena atrica*

Kind of anomaly	Number of individuals	%
Oligomely	28	70.0
Heterosymely	2	5.0
Schistomely	3	7.5
Symely	2	5.0
Bicephaly	1	2.6
Complex anomalies	4	10.0
Total	40	100.0

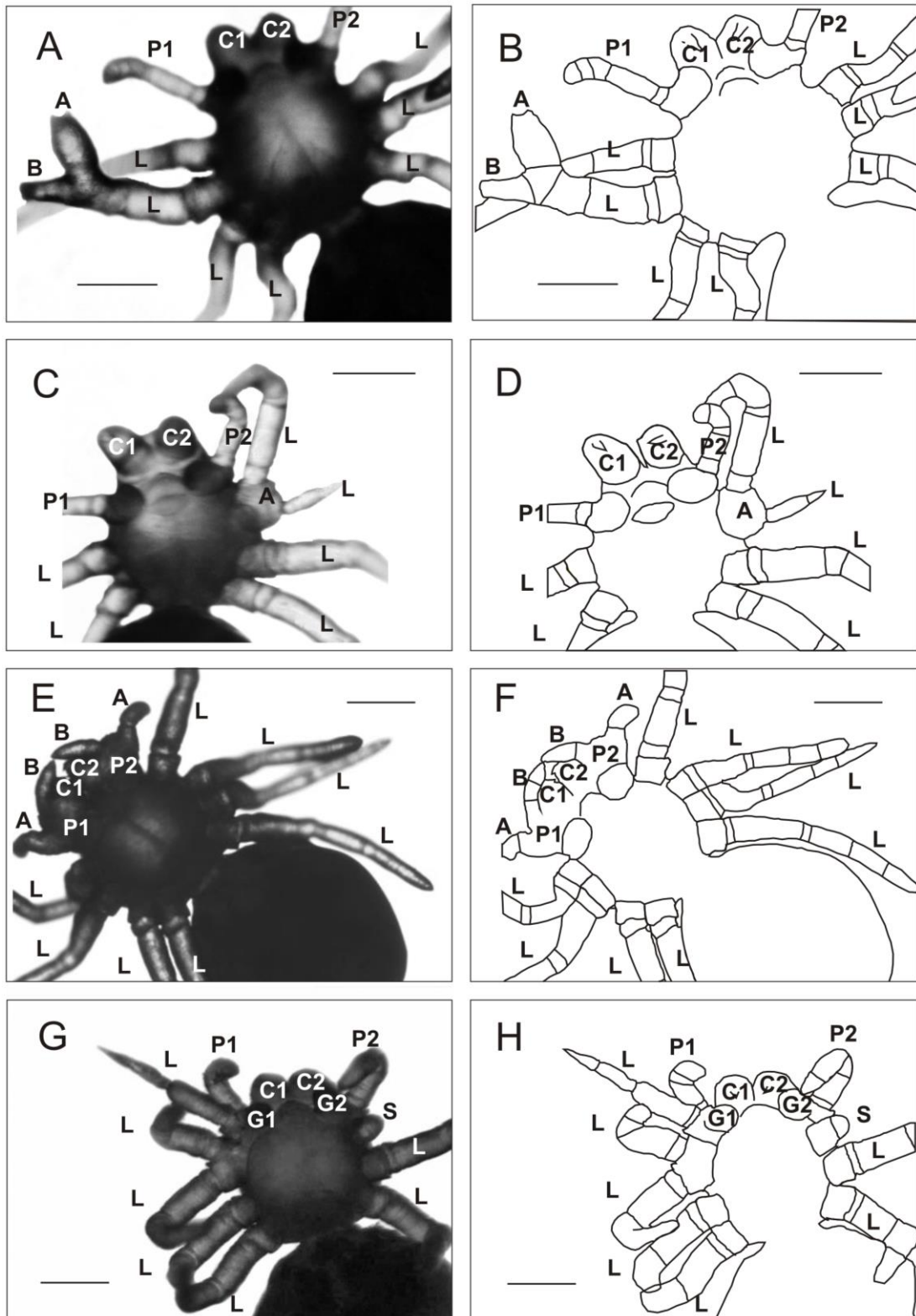


Fig. 1 *Eratigena atrica* larvae with developmental anomalies of the prosoma.

A, B = larva with oligomely and a forked walking leg (ventral view): A, B = forked ends; C1, C2 = chelicerae; L = walking legs; P1, P2 = pedipalps, Scale bar = 0.40 mm.

C, D = larva with oligomely, heterosymely and shortening of walking leg (ventral view): A = fused coxae, C1, C2 = chelicerae, L = walking legs; P1, P2 = pedipalps, Scale bar = 0.50 mm.

E, F = larva with heterosymely of chelicerae and schistomelic pedipalps (ventral view): A, B = forked ends of pedipalps; C1, C2 = chelicerae; L = walking legs; P1, P2 = pedipalps, Scale bar = 0.40 mm.

G, H = larva with oligomely, double heterosymely, polymely and short stump (ventral view): C1, C2 = chelicerae; G1, G2 = gnathocoxae; P1, P2 = pedipalps; L = walking legs, S = stump, Scale bar = 0.45 mm.

malformations (*i.e.*, oligomely, schistomely, heterosymely) had already been discussed in previous papers (*e.g.*, Jacuński *et al.*, 2005; Napiórkowska *et al.*, 2007, 2013), we decided to focus on four individuals with complex anomalies. These four cases differ significantly and are therefore analyzed separately.

Case 1. The spider in Figure 1 (A, B) was affected by two anomalies observed on two sides of the prosoma. On the right side of the prosoma (ventral side) there were only three walking legs (L) (unilateral oligomely). The deformity on the opposite side was more complex and therefore more difficult to classify. The second walking leg was slightly shorter and thicker than the others and had two ends (A, B). The ends were relatively short and had the same length but one (A) was massive and had two small protuberances. The free ends had a uniform structure and there were no visible articular surfaces on them. This anomaly may be classified in two ways: 1) as schistomely (bifurcation) 2) as polymely with partial heterosymely (one supernumerary walking leg and incomplete fusion of two others).

Case 2. The complex anomaly in the spider in Figure 1 (C, D) affected its walking legs and was very complicated. On the left side of the prosoma (ventral side) only two legs were fully developed (L) (oligomely). On the right side of the prosoma, apart from two well-developed walking legs (L), there were two appendages behind the pedipalp (P2). However, these two legs had the coxae fused into one large, massive structure (heterosymely) (A). The remaining part of one of these appendages was properly built, with six segments, but the other was teratogenically changed: it was significantly shorter, and consisted of only two narrow segments. Unilateral lack of legs caused significant asymmetry of the prosoma.

Case 3. The spider in Figure 1 (E, F) had anomalies in the anterior part of the prosoma. The anomalies affected its chelicerae and pedipalps. Both chelicerae (C1 and C2) were partially fused (heterosymely) with schistomelic pedipalps (P1 and P2). Deformities of the pedipalps were identical. Forked ends of both pedipalps (A and B) were of equal length and width and consisted of three parts: patella, tibia and tarsus. The ends of the legs moved independently. These teratogenically changed pedipalps with well developed gnathocoxa merged with chelicerae. The fusions on the right and left part of the prosoma were identical. Heterosymely affected half of the base part of each chelicera and the first three segments of each pedipalp. The remaining part of the chelicerae including claws were not fused.

Case 4. The spider in Figure 1 (G, H) had several deformities affecting its walking legs: oligomely, double heterosymely, polymely. Moreover, one leg was much shorter and another was not well-developed. On the right side of the prosoma (ventral side), there were only two fully developed legs with seven parts (L). Before them, behind the pedipalp (P2), was a short stump (S), probably a considerably shortened walking leg. On the other side of the prosoma behind the pedipalp (P1) were five walking legs (L); one was

supernumerary (polymelic). The first was shorter and thinner than the others. Its first three segments (coxa, trochanter, and femur) were well-developed, while the remaining ones were teratogenically changed: they were considerably narrower, with indistinct segmentation. Moreover, the coxa of this leg was fused with the coxa of the pedipalp (P1) (heterosymely). The coxae of the two next legs on this side of the prosoma were also fused (heterosymely). The remaining parts of these legs were properly developed.

Discussion

The results of the experiment confirm the hypothesis that temperatures of 14 and 32 °C used alternately have a significant impact on the mortality of embryos of *E. atrica* and the number of morphological deformities.

Oligomely (absence of legs) was the most frequent. It was identified in 70 % of individuals affected by deformities. Other anomalies, including complex ones (10 %), occurred with a significantly lower frequency. In total, specimens with morphologic changes constituted approx. 10 % of all individuals which hatched in this experiment. The number of individuals with anomalies would probably have been larger but the mortality of embryos was very high. We assume that the majority of embryos died in the early stages of embryogenesis due to extensive deformities. Others, although successfully completed embryonic development, could not leave the egg shells because of developmental defects. In the teratological material we found heavily deformed embryos, which did not leave the chorion. It can thus be concluded that serious leg deformities prevented them from hatching. The question then arises why the remaining 90 % of individuals from the experimental group did not show any changes. The possible explanation lies in efficient repair mechanisms that can effectively eliminate at least some of the deformities.

Our results indicate that organs of locomotion are most susceptible to developmental abnormalities. It may be connected with the fact that they are less vital for survival than, for example, chelicerae. In addition, it is believed that the thorax, with its metameric structure, is more primal and more prone to teratogenic effects of temperature (Jacuński, 1984; Jacuński *et al.*, 2004). Moreover, simple leg anomalies are not life threatening for a spider. As indicated by Jacuński *et al.* (2005), individuals without one or two legs can still build webs, hunt and molt, even though their fitness is severely impaired. Similar observations were made by Pechmann *et al.* (2011). It should also be noted that a majority of the anomalies consisted of one type of deformity. Complex anomalies were identified only in four individuals. In two cases deformities affected only walking legs (Figs 1 A, B and C, D). It seems that in one specimen (Figs 1A, B) the defect was not very severe: only one leg was missing, and the other was slightly shorter and thicker than the remaining ones. Two free ends in the distal part of this leg could indicate light schistomely. However, it cannot be ruled out that

these were actually two not fully fused legs. This would indicate the presence of two anomalies on one side of the prosoma: polymely and partial heterosymely. Of these two possibilities, schistomely is a less severe option. The results obtained by Napiórkowska *et al.* (2007) demonstrate that schistomely is subject to spontaneous processes of repair: after several molts the defect is eliminated. Furthermore, after the bifurcated end of the appendage is amputated, the damage is repaired as a result of epimorphic processes. The affected spider can lead a normal life. However, in the second case (Figs 1C, D) the defect seems more serious. A higher number of missing legs combined with heterosymely (fusion of legs) significantly impaired the symmetry of the prosoma and influenced molting of this individual. During the first post-larval molt the deformed leg detached. This led to a large loss of hemolymph and caused the death of the spider. It should be noted that the change which we identify as heterosymely resembles a biramous leg. In arthropods a biramous leg is considered primal, so, it can be viewed as a possible return to ancestry. Similar conclusions were made by Jacuński (1971, 1984, 2002) and Templin *et al.* (2009-2010) who investigated larvae of *E. atrica* with appendages on petiolus (the first segment of the opisthosoma) or in place of book lungs as well as larvae with a change in the opisthosoma resembling postabdomen. According to these authors, alternating temperatures impairing embryonic development, caused a return to phylogeny and atavism (the appearance of traits belonging to ancestors).

Of the two remaining cases of complex anomalies, one affected only pedipalps and chelicerae (Figs 1E, F), while the other affected walking legs and a pedipalp (Figs 1G, H). Case 3 is particularly interesting (Figs 1E, F). This type of deformity was identified for the first time in the history of teratological studies. The deformity affected pedipalps and chelicerae on both sides of the prosoma in exactly the same way. Before, Jacuński *et al.* (2002a) reported one case of unilateral heterosymely of these appendages. Histological analysis then revealed a change in the position of a venom gland, which was contained entirely within the fused appendages and shifted towards the pedipalp. The specimen in Case 4 (Figs 1G, H) had six abnormalities, which affected legs on the prosoma. Although extremely rare, such anomalies have already been described by Jacuński and Napiórkowska (2000) and Jacuński *et al.* (2004).

It would be very interesting to understand why these abnormalities developed. According to Rousseaux (1988) abnormal phenotypes are the results of the genetic constitution of an animal and the molecular, cellular, and histogenic environment in which they grow. For normal development, the critical cellular mass, correct cellular induction and movements must occur at the proper time and place. Mutations, chromosomal aberrations, and environmental interactions with genes that produce abnormal development may initially produce abnormal cells and later a phenotypically abnormal

individual. It could be assumed that anomalies that we observed in spiders result from changes in the movement or death of cells caused by alternating temperatures or displacement or dislocation of the cumulus in blastoderm stages. However, based on latest reports (*e.g.*, Damen *et al.*, 1998; Telford and Thomas, 1998; Pechmann *et al.*, 2009; Schwager *et al.*, 2009; Khadjeh *et al.*, 2012) we suppose that these deformities result from changes in *Hox* gene expression patterns. *Hox* genes are able to alter the arthropod plan. *Hox* genes encode transcription factors and are expressed in partially overlapping expression domains along the anterior-posterior body axis. These genes determine the presence or absence of legs in different parts of the body. One of them is *Antennapedia* gene (*Antp*), whose expression pattern in *A. tepidariorum* suggests a role in leg repression rather than in leg development (Khadjeh *et al.*, 2012). It can therefore be assumed that in the deformed spider shown in Figs 1G, H there was, among other things, a variation in the expression pattern of this gene, and this led to the development of a supernumerary leg.

Another homeobox gene which is well known for its role in appendage formation is *Distal-less* (*Dll*) gene. The results of Pechmann *et al.* (2011) suggest that the early expression of *At-Dll* in the germ disc is required for the formation of L1 and L2 segments. The loss of early *At-Dll* function leads to malformation of the L1 and L2 segments and a large portion of the cells in these malformed segments is later removed by cell death. Moreover, the cell death apparently removes more cells in this region, resulting in the animals lacking both L1 and L2. Therefore, in case of oligomely (absence of walking legs), identified in three individuals (Figs 1A, B; C, D and G, H), there might have been a change in the expression of the *Hox* (*Dll*) gene responsible for the formation of segments and the entire appendages. Without sufficient research we were unable to determine which ones were lost, and we therefore marked them with the letter L only.

In the natural environment many factors may influence embryogenesis of spiders. Body deformities and changes in the internal structure are common results. It should be stressed that temperature affects not only the embryogenesis, but also biology of spiders and other invertebrates. Moreover, it determines the distribution and dynamics of entire populations (Ahmad *et al.*, 2016; Elekcioglu, 2017; Khan and Naveed, 2017). Unquestionably, complex anomalies described above were induced by the application of alternating temperatures during the first ten days of embryonic development. Deformities of this kind prevent spiders from leading a normal life not only in the environment, but also in the laboratory under the supervision of researchers. Extensive changes in spiders' morphology can seriously impair their life processes, eventually leading to their death. They do not have a chance to reach sexual maturity and reproduce. It should be accentuated that climate change and extreme weather events may result in a growing number of serious deformities in spiders in the natural environment.

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References

- Ahmad T, Hassan MW, Jamil M, Iqbal J. Population dynamics of aphids (Hemiptera: Aphididae) on wheat varieties (*Triticum aestivum* L.) as affected by abiotic conditions in Bahawalpur, Pakistan. *Pakistan J. Zool.* 48: 1039-1044, 2016.
- Aitchison CW. Feeding and growth of *Coelotes atropos* (Araneae, Agelenidae) at low temperatures. *J. Arachnol.* 9: 327-330, 1981.
- Asiain J, Márquez J. New teratological examples in neotropical Staphylinidae (Insecta: Coleoptera), with a compilation of previous teratological records. *Rev. Mex. Biodivers.* 80: 129-139, 2009.
- Barghusen LE, Claussen DL, Anderson MS, Bailer AJ. The effects of temperature on the web-building behavior of the common house spider, *Achaearanea tepidariorum*. *Funct. Ecol.* 11: 4-10, 1997.
- Buczek A. Oligomely of legs in larvae of *Hyalomma marginatum* Koch, 1844 (Acari: Ixodida, Ixodidae). *Przegl. Zool.* 36: 251-253, 1992.
- Buczek A. Experimental teratogeny in the tick *Hyalomma marginatum marginatum* (Acari: Ixodida: Ixodidae): effect of high humidity on embryonic development. *J. Med. Entomol.* 37: 807-814, 2000.
- Cobb VA. Effects of temperature on escape behavior in the cribellate spider, *Oecobius annulipes* (Araneae, Oecobiidae). *Southwest. Nat.* 39: 392-394, 1994.
- Costa FG, Sotelo FG. Influence of temperature on the copulation duration of *Lycosa malitiosa* Tullgren (Araneae, Lycosidae). *J. Arachnol.* 12: 273-277, 1984.
- Ćurčić BPM, Krunić MD, Brajković MM. Tergal and sternal anomalies in *Neobisium* Chamberlin (Neobisiidae, Pseudoscorpiones, Arachnida). *J. Arachnol.* 11: 243-250, 1983.
- Damen WGM, Hausdorf M, Seyfarth EA, Tautz D. A conserved mode of head segmentation in arthropods revealed by the expression pattern of Hox genes in a spider. *Proc. Natl. Acad. Sci. USA* 95: 10665-10670, 1998.
- Darymple SE. The effect of temperature on the development rate of *Anelosimus studiosus*. University of Tennessee Honors Thesis Projects, 2005.
- Davis D. The effects of temperature on courtship behavior of the wolf spider *Schizocosa rosneri* (Araneae: Lycosidae). *Am. Midl. Nat.* 122: 281-287, 1989.
- Downes MF. The effect of temperature on oviposition interval and early development in *Theridion rufipes* Lucas (Araneae, Theridiidae). *J. Arachnol.* 16: 41-45, 1988.
- Eeva T, Penttinen R. Leg deformities of oribatid mites as an indicator of environmental pollution. *Sci. Total Environ.* 407: 4771-4776, 2009.
- Elekcioğlu NZ. Effect of different temperatures on the biology of *Citrostichus phyllocnistoides* (Narayanan) (Hymenoptera: Eulophidae) a parasitoid of *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae). *Pakistan J. Zool.* 49: 685-691, 2017.
- Fernandes CS, Gregati RA, Bichuette ME. The first record of external abnormalities in the subterranean *Aegla marginata* Bond-Buckup & Buckup, 1994 (Crustacea: Decapoda: Aegliidae), from a karst area of Southeastern Brazil. *Subterr. Biol.* 8: 33-38, 2010.
- Gregati RA, Negreiros-Fransozo ML. Occurrence of shell disease and carapace abnormalities on natural population of *Neohelice granulata* (Crustacea: Varunidae) from a tropical mangrove forest, Brazil. *Mar. Biodivers. Re.* 2: 1-3, 2009.
- Hanna ChJ, Cobb VA. Effect of temperature on hatching and nest site selection in the Green lynx spider, *Peucetia viridans* (Araneae: Oxyopidae). *J. Therm. Biol.* 31: 262-267, 2006.
- Ito T, Sekiguchi K. Induction of multiple embryos with NaHCO₃ or calcium free sea water in the horseshoe crab. *Wilhelm Roux's Arch.* 189: 245-254, 1979.
- Ito T, Sekiguchi K. Morphogenic movement and experimentally induced decrease in number of embryonic segments in the Japanese horseshoe crab, *Tachypelus tridentatus*. *Biol. Bull.* 158: 324-338, 1980.
- Jacuński L. The effect of temperature treatment at various stages of embryonic development on formation of monstrosities in the spider *Tegenaria atrica* C. L. Koch. *Bull. Acad. Polon. Sci. Cl.* 9: 555-556, 1969.
- Jacuński L. Temperature induced developmental monstrosities in *Tegenaria atrica* C. L. Koch (Araneae, Agelenidae). *Zool. Polon.* 21: 285-316, 1971.
- Jacuński L. Studia nad teratogenezą eksperymentalną u pająka *Tegenaria atrica* C.L.Koch. UMK Toruń, 1984.
- Jacuński L. Anomalies of the abdomen in *Tegenaria atrica* C.L.Koch (Araneae, Agelenidae). *Bull. Pol. Ac. Sci. Biol. Sci.* 50: 183-188, 2002.
- Jacuński L, Napiórkowska T. Epimorphic regeneration of an appendage complex in *Tegenaria atrica* C. L. Koch (Agelenidae). *Bull. Pol. Ac. Sci. Biol. Sci.* 48: 269-271, 2000.
- Jacuński L, Napiórkowska T, Templin J. Heterosymely od mouth appendages in *Tegenaria atrica* C. L. Koch. *Bull. Pol. Ac. Sci. Biol. Sci.* 50: 189-191, 2002a.
- Jacuński L, Napiórkowska T, Templin J, Teszner L. Interesting cases of polymely in *Tegenaria atrica* C. L. Koch (Agelenidae). *Bull. Pol. Ac. Sci. Biol. Sci.* 50: 149-151, 2002b.
- Jacuński L, Napiórkowska T, Templin J, Teszner L. Anomalies in the cephalic part of prosoma in *Tegenaria atrica* C. L. Koch. *Zool. Polon.* 49: 97-100, 2004.
- Jacuński L, Templin J. Morphology of prosoma in bicephalous monsters of *Tegenaria atrica* C. L. Koch. *J. Therm. Biol.* 28: 393-396, 2003.

- Jacuński L, Templin J, Napiórkowska T. Dubling of prosoma in larva of *Tegenaria atrica* C. L. Koch (Agelenidae). Bull. Pol. Ac. Sci. Biol. Sci. 50: 85-87, 2002c.
- Jacuński L, Templin J, Napiórkowska T. Changes in the neuromerism of the subesophageal part of the nervous system in oligomelic individuals of *Tegenaria atrica* (Arachnida). Biol. Bratisl. 60: 589-592, 2005.
- Jacuński L, Wiśniewski H. The influence of temperature on the duration of embryonic stages of *Tegenaria atrica* C.L.Koch (Agelenidae). Sci. Pap. Pedagog. Univ. Nat. Stud. Bydgoszcz 13: 181-203, 1997.
- Janssen R. Developmental abnormalities in *Glomeris marginata* (Villers 1789) (Myriapoda: Diplopoda): implications for body axis determination in a myriapod. Naturwissenschaften 100: 33-43, 2013.
- Jara CG, Palacios VL. Occurrence of conjoined twins in *Aegla abtao* Schmitt, 1942 (Decapoda, Anomura, Aeglidae). Crustaceana 74: 1059-1065, 2001.
- Juberthie C. Etude des symélie provoquées par la température chez un Opilions (Arachnides). Comptes Rendus Acad. Sci. 254: 2674-2676, 1962.
- Juberthie C. Production expérimentale de l'hétérosymélie chez un Opilion. Comptes Rendus Acad. Sci. 256: 3363-3365, 1963a.
- Juberthie C. Monstruosités observées chez les Opilions. Bull. Mus. Natl. Hist. Nat. B 35: 167-171, 1963b.
- Khadjeh S, Turetzek N, Pechmann M, Schwager EE, Wimmer EA, Damen WGM, Prpic N-M. Divergent role of the Hox gene *Antennapedia* in spiders is responsible for the convergent evolution of abdominal limb repression. Proc. Natl. Acad. Sci. USA 109: 4921-4926, 2012.
- Khan RA, Naveed M. Occurrence and seasonal abundance of fruit fly, *Bactrocera zonata* Saunders (Diptera: Tephritidae) in relation to meteorological factors. Pakistan J. Zool. 49: 999-1003, 2017.
- Li D. Development and survival of *Erigonidium graminicolum* (Sundevall) (Araneae: Linyphiidae: Erigoninae) at constant temperatures. B. Entomol. Res. 85: 79-91, 1995.
- Li D. The combined effects of temperature and diet on development and survival of a crab spider, *Misumenops tricuspidatus* (Fabricius) (Araneae: Thomisidae). J. Therm. Biol. 27: 83-93, 2002.
- Małol J, Łaydanowicz J. Morphological abnormalities in terrestrial Parasitengona mites (Acari: Actinotrichida: Parasitengona). Biological Lett. 43: 131-143, 2006.
- Mikulska I, Jacuński L. A two-headed monster of the spider *Tegenaria atrica* C. L. Koch. Acta Arachnol. 23: 17-19, 1970.
- Mikulska I, Jacuński L. Dichotomy in embryos of the spider *Tegenaria atrica* C. L. Koch induced by supraoptimal temperature treatment in early embryogeny. Zool. Polon. 21: 281-284, 1971.
- Napiórkowska T, Jacuński L, Templin J. Epimorphosis and repair processes of schiostomelic pedipalps and walking appendages in *Tegenaria atrica* (Araneae, Agelenidae). Biol. Bratisl. 62: 756-762, 2007.
- Napiórkowska T, Jacuński L, Templin J. Polymely of feeding appendages in *Tegenaria atrica* (Araneae: Agelenidae). Bull. Br. Arachnol. Soc. 15: 52-54, 2010a.
- Napiórkowska T, Jacuński L, Templin J. An interesting case of a bicephalous *Tegenaria atrica* nymph. Bull. Br. arachnol. Soc. 15: 83-84, 2010b.
- Napiórkowska T, Napiórkowski P, Templin J. Morphological and anatomical changes related to leg anomalies in *Tegenaria atrica*. Zoomorphology 134: 237-245, 2015.
- Napiórkowska T, Napiórkowski P, Templin J. Teratological deformities of pedipalps in the *Tegenaria atrica* spider, induced by low and high temperatures applied alternately. J. Therm. Biol. 56: 50-54, 2016.
- Napiórkowska T, Templin J. Symely, a seldom occurring developmental anomaly in the spider *Tegenaria atrica*. Inv. Reprod. Dev. 57: 95-100, 2013.
- Napiórkowska T, Templin J, Napiórkowski P. The central nervous system of heterosymelic individuals of the spider *Tegenaria atrica*. Folia Biol. (Kraków) 61: 283-289, 2013.
- Pechmann M, Khadjeh S, Turetzek N, McGregor AP, Damen WGM, Prpic N-M. Novel function of *Distal-less* as a gap gene during spider segmentation. PLOS Genetics 7: 1-10, 2011.
- Pechmann M, McGregor AP, Schwager EE, Feitosa NM, Damen WGM. Dynamic gene expression is required for anterior regionalization in a spider. Proc. Natl. Acad. Sci. USA 106: 1468-1472, 2009.
- Pulz R. Thermal and water relations. In: Nentwig, W (ed), Ecophysiology of spiders. Springer-Verlag, Berlin Heidelberg New York London Paris Tokyo, pp 26-55, 1987.
- Punzo F. Spiders: biology, ecology, natural history and behavior. Brill, Leiden-Boston, 2007.
- Rousseaux CG. Developmental anomalies in farm animals. I. Theoretical considerations. Can. Vet. J. 29: 23-29, 1988.
- Rudolph EH, Martinez AW. Conjoined twins in the burrowing crayfish, *Virilastacus rucapihuelensis* Rudolph & Crandali, 2005 (Decapoda, Parastacidae). Crustaceana 81: 1347-1355, 2008.
- Schwager EE, Pechmann M, Feitosa NM, McGregor AP, Damen WGM. *hunchback* functions as a segmentation gene in the spider *Achaearanea tepidariorum*. Curr. Biol. 19: 1333-1340, 2009.
- Shelton PMJ, Truby PR, Shelton RGJ. Naturally occurring abnormalities (Bruchdreifachbildungen) in the chelae of three species of Crustacea (Decapoda) and possible explanation. J. Embryol. Exp. Morph. 63: 285-304, 1981.
- Spanò N, Ragonese S, Bianchini ML. An anomalous specimen of *Scyllarides latus* (Decapoda, Scyllaridae). Crustaceana 76: 885-889, 2003.
- Telford MJ, Thomas RH. Expression of homeobox genes shows chelicerate arthropods retain their deutocerebral segment. Proc. Natl. Acad. Sci. USA 95: 10671-10675, 1998.

Templin J, Jacuński L, Napiórkowska T. Disturbances in the structure of the prosoma in *Tegenaria atrica* induced by alternating temperatures (Araneae: Agelenidae). Bull. Br. Arachnol. Soc. 14: 303-307, 2009.

Templin J, Jacuński L, Napiórkowska T. Metameric malformations of opisthosoma in *Tegenaria atrica* (Araneae, Agelenidae). Zool. Polon. 54-55: 33-42, 2009-2010.