Revista Ibérica de Aracnología, nº **44** (30/06/2024): 166–171
Grupo Ibérico de Aracnología (S.E.A.). ISSN: 1576 - 9518.

Some teratological ocelli, chelicerae, legs and pectines in two tunisian *Scorpio* species (Scorpiones: Scorpionidae)

Manel Khammassi[1*] & Said Nouira[1]

[1] Research Unit of Wildlife Ecology, UR17-ES44, Faculty of Sciences of Tunis, University of Tunis El Manar, 2092 Tunis, Tunisia
*Corresponding author: manel.khammassi@fst.utm.tn ORCID : https://orcid.org/0000-0002-5523-3800
[2] : https://orcid.org/0000-0002-0412-6626

Abstract: Some cases of anomalies in the ocelli, chelicerae, legas and pectines of *Scorpio maurus* Linnaeus, 1758 and *Scorpio punicus* Fet, 2000 are described and illustrated. Those anomalies consit in unusual number and size of the ocelli, and legs, pectines and chelicerae malformations. The consequences of these teratological anomalies on the life of scorpions are finally discussed.
Key Words: Scorpion, *Scorpio*, anomalies, ocelli, appendages, Tunisia.

Anomalías en los ocelos, quelíceros, patas y peines en dos especies tunecinas de *Scorpio* (Scorpiones: Scorpionidae)
Resumen. Se describen e ilustran algunos casos de anomalías en los ocelos, los quelíceros, las patas y los peines de *Scorpio maurus* Linnaeus, 1758 y *Scorpio punicus* Fet, 2000. Dichas anomalías consisten en la pérdida o aumento del número de ocelos, así como en malformaciones de los apéndices (quelíceros, peines y patas). Se discute el posible efecto de tales anomalías en vida de los escorpiones.
Palabras clave: Escorpiones, *Scorpio*, anomalías, ocelos, apéndices, Túnez.

Introduction

Several anomalies have been widely described in different families of scorpions (Teruel, 2003; Mattoni, 2005; De Sousa *et al.*, 2009; Sherwood & Armas, 2023). The most common abnormalities are: duplication of certain parts of the body, like metasoma, pedipalp (Karataş & Kürtüllü, 2006; Seiter & Teruel, 2014; Salabi *et al*., 2021), and pectinal teratologies (Ayrey, 2011; Teruel & Baldazo-Monsivaiz, 2015; Šarić & Tomić, 2016). Other cases of morphological malformations, were reported, including malformations of the pectines (eg. De Sousa *et al*., 2009; Ayrey, 2011), legs and/or claws (eg. González-Sponga, 2004; David, 2012; Watz & Dunlop, 2020; Sherwood and Armas 2023), tergites (eg. Mattoni, 2005), chelicerae (eg. Yağmur *et al.,* 2021), and metasoma and/or telson (eg. Seiter & Teurel, 2014; Galvis & Flórez, 2016; Alqahtani & Badry, 2021; Sadine, 2021), but also sexual and developmental abnormalities have been described (eg. Mattoni, 2005). In the present work, we describe, for the first time, ocelli and other morphological anomalies in *Scorpio maurus* Linnaeus, 1758 and *Scorpio punicus* Fet, 2000 (family Scorpionidae) from Tunisia. We then discuss the consequences of these teratological anomalies on the life cycle of the scorpions and their taxonomic status.

Material and Methods

Specimens of two Tunisian *Scorpio* species were collected between January 2018 and October 2021, during day search by stone-turning and burrow-digging. They are preserved in 95% ethanol and deposited in the Collection of Scorpions at Research Unit of Ecology, Department of Biology, Faculty of Sciences of Tunis, Tunisia. Morphological terminology follows Vachon (1974) for trichobothrial notation; Loria and Prendini (2014) for the terminology of ocellus model; Birula (1910), Stahnke (1970), Vachon (1950), and Hjelle (1990) for remaining features. Measurements were taken as described in Vachon (1950) and Stahnke (1970), and are given in millimeters (mm).

Results and discussion

A15 out of 232 *Scorpio* specimens (142 of *S. maurus*, and 90 of *S. punicus*) showed various anomalies and malformations, as shown in the Table I.

1. Ocelli

Scorpions possess two types of visual organs: the median eyes, a single pair of ocelli, located dorsomedially on the carapace, except in 26 troglomorphic species; and the lateral eyes, located anterolaterally on each side of the carapace, except in 17 troglomorphic species (Mitchell, 1968; Sissom, 1988; Hjelle, 1990; Volschenk & Prendini, 2008; Lourenço, 2012). The number, position, and size of the lateral eyes vary and hold taxonomic significance (González-Sponga, 1977; Sissom, 1990; Loria & Prendini, 2014). Structural differences between median and lateral eyes result in differing functions: median eyes offer high visual acuity and spatial discrimination, while lateral eyes are highly sensitive and regulate circadian rhythms (Fleissner, 1977; Schliwa & Fleissner, 1980; Warburg & Polis, 1990; Lehmann & Melzer, 2013; Warburg, 2013).

The genus *Scorpio* is characterized by the presence of two median ocelli and three pairs of lateral ocelli. Vachon (1950) described these as "the two median eyes at the back [....], the two lateral eyes on either side of the scutum, the two larger anterior eyes being close to each other and distant from the smaller posterior eyes". According to Loria and Prendini (2014), the genus *Scorpio* has the pattern of lateral ocelli type 3A (Fig. 1A). This pattern is characterized by the presence of two major ocelli: the mediolateral major ocellus (MLMa) and the posterolateral major ocellus (PLMa), and one minor ocellus (the posterodorsal minor ocellus (PDMi)). However, the eyespot and three ocelli (anterolateral major ocellus (ALMa); anterodorsal minor ocellus (ADMi) and posterolateral minor ocellus (PLMi)) are absent.

Ocelli anomalies

In this study, seven *S. maurus* and three *S. punicus* specimens have ocelli anomalies that can be classified into three types:

1) A supernumerary ocellus: The specimen has a supernumerary lateral ocellus on one side with a variable size that increases the number of lateral ocelli from three to four ocelli. The extra lateral ocellus is located between the mediolateral major ocellus and the posterolateral major ocellus (Fig. 1B-C) or between the posterolateral major ocellus and the posterodorsal minor ocellus (Fig. 1D-E).

2) Atrophy of the ocelli: the two main ocelli have a very small size (Fig. 1F).

3)Absent ocelli: three lateral ocelli are missing (Fig. 1G).

The lateral ocelli are an important anatomical feature at the taxonomic level in the systematics of scorpions (Soleglad & Fet, 2003; Prendini & Wheeler, 2005; Loria & Prendini, 2014). The first case of ocelli anomalies was observed in *Cazierius gundlachii* (Karsch, 1880), characterized by the absence of one left ocellus and all three ocelli on the right side (Armas, 1976). Different cases of teratological ocelli in scorpions have been documented (Santiago-Blay, 1986; Gonzalez-Sponga, 2004; Sherwood & Armas, 2023). Here, different numbers of teratological ocelli were observed in *S. maurus* and *S. punicus*. Ecologically, the absence of ocelli, a sensitive organ, may impair the scorpions' activity, resting behaviors, and disrupt their circadian clock. Evolutionarily, the progressive loss of ocelli, considered an apomorphic character (Kjellesvig-Waering,

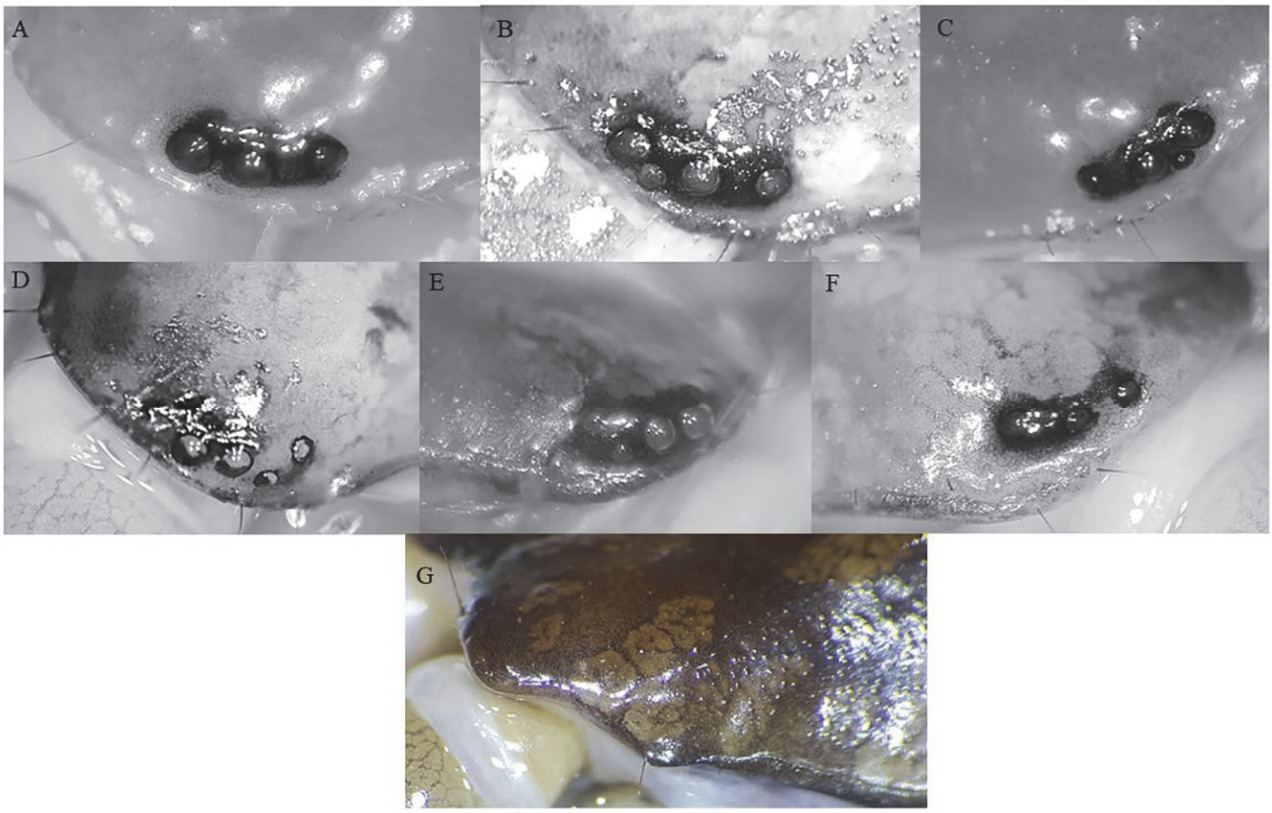

Figure 1: Ocelli anomalies in *Scorpio* species from Tunisia. (A) Three normal lateral ocelli. (B-C) The supernumerary lateral ocellus is located between mediolateral major ocellus and posterolateral major ocellus (left side : B; right side : C). (D-E) The supernumerary lateral ocellus is located between posterolateral major ocellus and posterodorsal minor ocellus (left side : D; right side : E). (F) Atrophy of the two major ocelli ocelli in the right side. (G) Absence of lateral ocelli in the left side.

Table I: Sampling sites of *Scorpio* species in Tunisia with anomalies and malformations remarks.

Specimens code	Species Scorpio sp.	Sexe	Stage	Nºof pectinal teeth	GPS coordinates		Locality	Organs with anomalies and malformations
MK027	*S. maurus*	♀	adult	10-10	35°52'N	9°27'E	Kesra forest	First left leg (tarse and basitarse fused), four left ocelli, pectinal teeth
MK113	*S. maurus*	♂	adult	8-9	36°49'N	8°41'E	Babbouch	First left leg (tarse and basitarse fused)
MK121	*S. maurus*	♂	adult	9-10	36°49'N	8°50'E	National Parc of Oued Ezzen	First left leg (tarse, basitarse and tibia fused)
MK135	*S. maurus*	♀	subadult	10-10	36°19'N	8°43'E	Essif Mountain	Four left ocelli
MK171	*S. maurus*	♂	juvenile	11-12	36°31'N	8°19'E	National Parc of El-Feija	Atrophy of left pecten
MK489	*S. maurus*	♀	adult	9-8	36°30'N	8°18'E	National Parc of El-Feija	Atrophy of two right lateral ocelli
MK497	*S. maurus*	♂	subadult	10-11	36°31'N	8°19'E	National Parc of El-Feija	Absence of left lateral ocelli
MK505	*S. maurus*	♀	juvenile	10-9	36°30'N	8°18'E	National Parc of El-Feija	Four right ocelli
MK536	*S. maurus*	♂	subadult	9-10	36° 6'N	9°37'E	Bargou Mountain	First left leg (tarse and basitarse fused)
MK378	*S. punicus*	♀	juvenile	10-10	34°31'N	8°41'E	El Guettar	Left cheliceral movable finger malformed
MK393	*S. punicus*	♀	adult	10-10	34°31'N	8°41'E	El Guettar	Four right ocelli
MK561	*S. punicus*	♂	juvenile	11-11	34°31'N	8°41'E	El Guettar	Four left ocelli
MK710	*S. punicus*	♂	subadult	11-11	34°31'N	8°41'E	El Guettar	Second right leg (tarse and basitarse fused)
MK643	*S. punicus*	♀	juvenile	11-10	34°44'N	9°35'E	El Meknassi	Second left leg (tarse and basitarse fused)
MK712	*S. punicus*	♀	adult	11-0	34°59'N	9°39'E	Regueb	Absence of left pecten

1986; Sissom, 1990; Bitsch & Bitsch, 2005), has decreased the number of lateral eyes since the Paleozoic era, leading to the aggregate eyes seen in extant scorpions. The origin of these teratological eyes remains unknown.

2. Chelicerae

Chelicerae are composed of three articles: the basal segment or coxa, the tibia with its fixed finger and the tarsus or movable finger. In the genus *Scorpio*: from tip to base, the cheliceral fixed finger with distal (d), subdistal (sd), median (m), and basal (b) teeth fused into a fork. Movable finger with the distal internal tooth (di) and the distal (d), subdistal (sd), median (m), and basal (b) teeth (Vachon, 1963; Hjelle, 1990; Sissom, 1990; Soleglad & Fet, 2003).

Cheliceral malformation

A short left cheliceral mobile finger with the anomaly of the cheliceral teeth was found in one immature female of *S. punicus* in this study. The basal tooth (b) is absent. The distal tooth (d), the subdistal tooth (sd) and the median tooth (m) are very weakly developed and are represented by a small dentition. Subdistal tooth is closer to median tooth than to distal tooth. The distal internal tooth (di) is very short and slightly curved (Fig. 2). The right cheliceral movable

Figure 2: Left cheliceral movable finger malformed

finger is normal. Both chelicerae have a normal cheliceral fixed finger with normal dentition, and normal tibia.

The first case of cheliceral malformation was reported in *Centruroides guanensis* Franganillo, 193, in which the left chelicera had a supernumerary tooth in the ventral border (Armas,1977). Several species of scorpions with different types of cheliceral anomalies have been observed (Santiago-Blay, 1986 ; Armas & Marcano Fondeur, 1992 ; Teruel, 2003 ; Teruel & Ove Rein, 2009 ; Tate *et al*., 2013 ; Yağmur *et al*., 2021; Sherwood & Armas, 2023).

The movements of the scorpion's chelicerae are brought about by 18 different muscles. The movable finger has a strong adductor (closing) muscle and a relatively weak abductor (opening) muscle (Vyas, 1974). Therefore, the cheliceral movable finger appears to have a critical function in the capture of prey and the feeding of scorpions (Hjelle, 1990).

This study documents the first case of a cheliceral anomaly in the movable finger of *S. punicus*, potentially limiting its functionality and negatively impacting the scorpion's ability to feed. Furthermore, the presence/absence, position, and shape of the cheliceral dentition have been used to classify families and provide important taxonomic features of scorpions (Vachon, 1963; San-martin & Cekalovic, 1972; Soleglad & Fet, 2003).

3. Legs

The legs are locomotory appendages with seven segments: the coxa, trochanter, femur, patella, tibia, basitarsus, and tarsus, ending with the apotele, which consists of the lateral claws and the median claw (dactyl) (Vachon, 1957; Couzijn, 1975; Hjelle, 1990). In addition, the legs are mechanosensory organs by comprising three types of sensory organs: first, the proprioceptors, formed by the slit sensilla; second, the sensory projections, divided into two groups: immovable projections or spines and mobile projections or setae; finally, the sensory organ or basitarsal compound slit sensillum (BCSS), located just above the tarsal hinge (Barth & Wadepuhl, 1975; Bowerman & Burrows, 1980; RooT & Bowerman, 1981; Hjelle, 1990).

Leg malformations

Leg malformations were observed in three *S. maurus* and two *S. punicus* specimens. An adult female *S. maurus* has a right first leg malformation (Fig. 3A): tarsus and basitarsus fused into a small segment. Lateral claws and dactyl are short, spurs very small or absent. An adult male *S. maurus* has a first left leg malformation (Fig. 3B): tarsus and basitarsus completely fused forming a very short segment (1.7 mm in length). The apotele has a short dactyl and lateral claws, spurs are small. Tibia is short.

A subadult female of *S. maurus* has a malformation of the left first leg (Fig. 3C): tarsus, basitarsus and tibia are absent, represented by a tiny segment with an anterodorsal depression, length about 2.2 mm. Lateral claws are developed and the dactyl is very small. Spurs are missing and seem to be replaced by long macrochaetae. The patella has several long macrochaetae. In a subadult male *S. punicus*, the second right leg is malformed (Fig. 3D): the tarsus and basitarsus are completely fused, forming a short segment (1.8 mm long). The apotele has a short dactyl and well-developed lateral claws. Spurs and tibia are normal. A juvenile female of *S. punicus* has a malformation of the second left leg (Fig. 3E): the tarsus and the basitarsus are completely fused into a short segment. Lateral claws are long, middle claw short. The number of the spurs is reduced.

The first case of a missing leg has been reported in *Androctonus australis* (Linnaeus, 1758), with a third leg malformed from femur downwards, with abnormal growths, the apical growth with distal claws (Vachon,1946). In the present work, anomalies at the terminal segments of the first and second legs in scorpion species have been described. Similar malformations have been described in several scorpions species such as: *Centruroides guanensis* Franganillo, 1931 (Armas, 1977), *Heteronebo portoricensis* Francke, 1978 (Santiago-Blay, 1986), *Microtityus barahona* Armas & Teruel, 2012 (Armas & Marcano Fondeur, 1992), *Rhopalurus laticauda* Thorell, 1876, *Chactas gansi* González-Sponga, 1974 (González-Sponga, 2004), and recently *Pandinurus pallidus* (Kraepelin, 1894) (Sherwood & Armas, 2023)

In scorpions, functional leg morphology and musculature are adaptations to burrowing and subterranean life (Couzijn, 1975). Anatomical differences between leg I and IV imply different functionality due to leg position, while legs II and III are always intermediate in shape and position. Leg I function as a tactile and burrowing organ and contributes little to locomotion. However, the main function of leg IV in this activity is to put forth in the propulsion backstroke (Couzijn, 1975; Hembree *et al*., 2012). The terminal part is directed rostrally in the leg I and it is directed caudo-ventrally in the leg IV. The position, rotation, and shape of the terminal part define its functions, most importantly, contact with the substrate (Manton & Harding, 1958; Couzijn, 1975; Bowerman & Burrows, 1980).

In this study, the teratological end segments consist of a complete fusion of basitarsus and tarsus. This leads to the absence of the BCSS. The absence of such a sensory organ could limit the ability of the scorpion to move and to detect prey and predators (Krapf, 1986). In addition, legs with these anomalies are shorter than normal legs. Burrowing scorpions use their first and second legs to dig. The shortening of the first or the second leg could affect the ability of the scorpions to dig and could imply more energy and more time for the excavation. Interestingly, the terminal part is narrow. This anomaly could be a limitation of the scorpion's movement during climbing and walking on irregular surfaces.

4. Pectines

The pectens are an autapomorphic character of the scorpion that has evolved during the Silurian period (Kjellesvig-Waering, 1986; Wendruff *et al*., 2020). Anatomically, these double comb-like organs are situated at the ventral side of the mesosoma. Each pecten consists of three marginal lamellae with a variable number of median lamellae, fulcrae, and pectinal teeth (Ivanov & Balashov, 1979; Hjelle, 1990; Melville, 2000). In addition, the number of pectinal teeth is generally species-specific (Birula, 1910; Vachon, 1950). The pectines are sensory organs with a primary function as mechanoreceptors and chemoreceptors. This function is performed by three different sensory structures: macrosetae, microsetae, and peg-shaped sensilla (Ivanov & Balashov, 1979; Foelix & Muller-Vorholt, 1983; Gaffin & Walvoord, 2004; Wolf, 2017; Drozd, 2019).

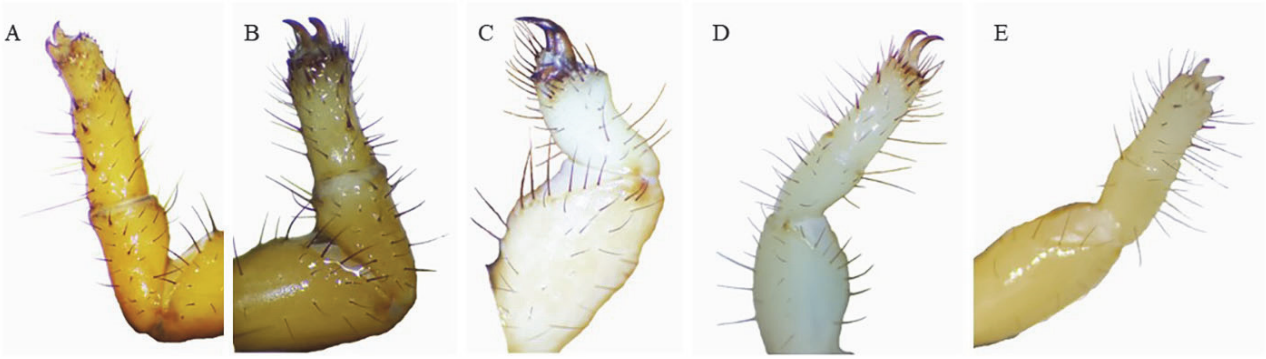

Figure 3: Legs malformations in *Scorpio* species from Tunisia. (A) First right leg of an adult female *S. maurus* with fusing tarsus and basitarsus. (B) First left leg of an adult male *S. maurus* with fusing tarsus and basitarsus. (C) First left leg of subadult female *S. maurus* with tarsus, basitarsus and tibia fused. (D) Second right leg of subadult male *S. punicus* with fusing tarsus and basitarsus. (E) Second left leg of juvenile female *S. punicus* with fusing tarsus and basitarsus.

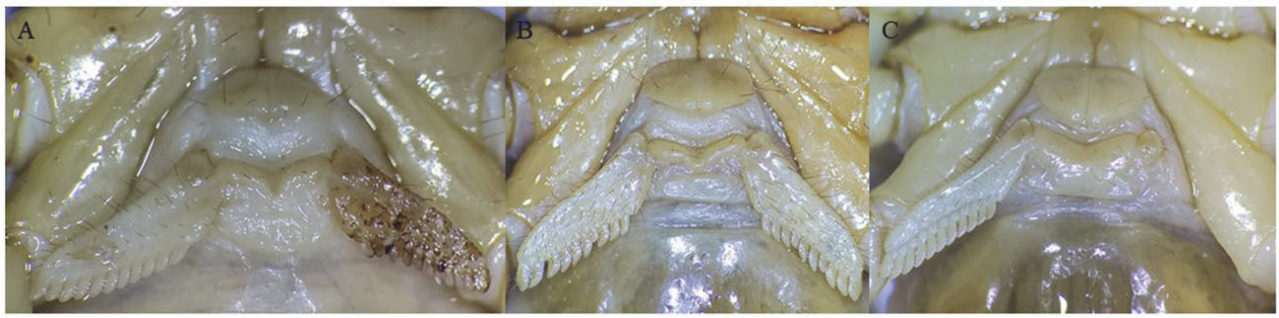

Figure 4: Pectines anomalies in *Scorpio* species from Tunisia. (A) Atrophy of left pecten of juvenile female *S. maurus*. (B)Anomalies in pectinal teeth of an adult female *S. maurus*. (C) Absence of the left pecten in an adult female *S. punicus*.

Pectinal teratology

Two *S. maurus* and one *S. punicus* specimens exhibit pectine malformations. The juvenile female *S. maurus* has markedly abnormal pectines (Fig. 4A), showing significant asymmetry between the right and left pectines, measuring 6/4.4/2.5 mm and 5.5/4/2 mm respectively. The left pecten is shorter and smaller than typical for this species, with a brownish-black coloration and black spots indicating lost setae insertions. All pectinal teeth are small, and the fifth and tenth teeth display brownish-black coloration with necrotic zones. The surface area of the anteroventral margin, known as peg sensilla, of the remaining pectinal teeth is reduced, and the number of sensilla per peg sensilla is lower than normal. An adult female *S. maurus* also presents pectine abnormalities (Fig. 4B). In this specimen, the first and tenth teeth of the left pecten are small, with the seventh tooth being very short. On the right pecten, the fourth and seventh teeth are tiny, and the last three teeth are small. These malformed teeth have significantly altered sensory areas; the peg sensilla are greatly reduced and cylindrical with blunt tips. Another notable anomaly is the absence of the left pecten in an adult female *S. punicus* (Fig. 4C).

In the first case, the pecten exhibited atrophy and necrosis aspect, likely due to a fungal infection or parasitic injury. Other environmental factors, such as injury during early ontogenesis or exposure to mutagenic/toxic substances, could also be responsible for this atrophy (Šarić & Tomić, 2016). Genetic alterations, possibly mutations or chromosomal aberrations, may explain the second and third cases of teratological pecten observed in this study. Similar cases of abnormal pecten with numerous teeth of irregular shape has been observed in *Tityus clathratus* C. L. Koch, 1845, *Broteas* sp, and *Opisthacanthus* sp. (González-Sponga, 2004), *Tityus quirogae* De Sousa, Manzanilla, Parrilla-Álvarez, 2006 (De Sousa *et al*., 2009), and missing pectines have been reported in *Centruroides gracilis* (Latreille, 1804) (Martín-Frías *et al*., 2009). Other cases of malformed pectines have been reported (De Sousa *et al*., 2009; Ayrey, 2011; Šarić & Tomić, 2016; Sherwood & Armas, 2023), typically involving partially or almost completely fused pectinal structures. One case of pectine duplication has also been documented (Teruel & Baldazo-Monsivaiz, 2015).

Except for the first case in this study, all teratological pectines suggest genetic origins during embryogenesis or chromosomal aberrations in gametes during meiosis. The functionality of the pecten, a highly innervated organ, has long been discussed and various functions have been attributed to it (Cloudsley-Thompson, 1955; Ivanov & Balashov, 1979; Foelix & Muller-Vorholt, 1983).

Later, it was concluded that the main function of the pectines is chemosensation and mechanoreception (Wolf, 2008, 2017; Drozd, 2019), based on behavioral, morphological and physiological studies. This dual function of pectines allows scorpions: mating activity, habitat selection, and orientation in their environment (Wolf, 2017; Drozd, 2019). An important common point in the pectinal anomalies described in this study is the reduction of the surface of the peg sensilla and the number of sensillum, which leads to the absence of environmental signals. Consequently, the fitness of these individuals could be severely compromised.

Conclusion

In conclusion, the study of anomalies and malformations, particularly in scorpions, is of significant interest for two main reasons. Firstly, it enhances our understanding of the morphological variability of each organ, which is crucial for systematics. Secondly, examining these anomalies provides insights into the functionality of each structure and its impact on the fitness of the scorpion. This study describes the teratology of ocelli, legs, chelicerae, and pecten in *S. maurus* and *S. punicus*, highlighting potential effects on the scorpions' vital activities. Consequently, future research should focus on genetic diversity and karyotype analysis to gain deeper insights into developmental genes.

Acknowledgments

This work is part of PhD thesis of the first author. MK thanks members of Research Unit of Wildlife Ecology, Faculty of Sciences of Tunis, University of Tunis El Manar, for their kindness and their help. MK is indebted to many local authorities for providing permits to carry out the research,

especially “Direction Générale des Forêts” (Tunisia). Also, MK acknowledge all engineers and technicians of ‘Direction Générale des Forêts’ (Tunisia) for help in the field and with logistics.

References

ALQAHTANI, A. R. & BADRY, A. 2021. A rare telson anomaly in *Parabuthus liosoma* (Ehrenberg, 1828) (Scorpiones: Buthidae). *Euscorpius*, **336**:1-4.

ARMAS, L. F. DE. 1976. Escorpiones del archipiélago cubano. Familia Diplocentridae (Arachnida: Scorpionida). *Poeyana*, **147**: 1–35.

ARMAS, L. F. DE 1977. Anomalías en algunos Buthidae (Scorpionida) de Cuba y Brasil. *Poeyana*, **176**: 1–6.

ARMAS, L. F. de & MARCANO FONDEUR, E. J. 1992. Nuevos alacranes de República Dominicana (Arachnida: Scorpiones). *Poeyana*, **420**: 1–13.

AYREY, R. F. 2011. An anomaly of pectinal organs in *Vaejovis lapidicola* (Scorpiones: Vaejovidae). *Euscorpius*, (**130**):1-6. DOI :

BARTH, F. G. & WADEPUHL, M. 1975. Slit sense organs on the scorpion leg (*Androctonus australis* L., Buthidae). *Journal of Morphology*, **145**(2):209-227.

BIRULA, A. 1910. Ueber *Scorpio maurus* Linné und seine Unterarten. *Horae Societatis Entomologicae Rossicae*, **39**:115-192.

BITSCH, C. & BITSCH, J. 2005. Evolution of eye structure and arthropod phylogeny. In: Koenemann, S. & Jenner, R. (ed) Crustacea and Arthropod Relationships. *Crustacean Issues*, **16**:185-214.

BOWERMAN, R. F. & BURROWS M. 1980. The morphology and physiology of some walking leg motor neurones in a scorpion. *Journal of Comparative Physiology*, **140**:31–42.

CLOUDSLEY-THOMPSON, J. L. 1955. On the function of the pectines of scorpions. *Annals and Magazine of Natural History*, **8**(91):556-560. COUZIJN, H. 1975. Functional anatomy of the walking-legs of Scorpionida with remarks on terminology and homologization of leg segments. *Netherlands Journal of Zoology*, **26**(4):453-501, 1975. DAVID, D. 2012. A seven-legged scorpion: the first teratological leg absence found in *Scorpio maurus fuscus* (Scorpiones: Scorpionidae). *Euscorpius*, (**151**):1-4.

DE SOUSA, L., VASQUEZ-SUAREZ, A., MANZANILLA, J. & GREGORIANI, T. 2009. Alteraciones morfológicas observadas en el escorpión *Tityus quirogae* (Scorpiones, Buthidae) del nordeste de Venezuela. *Bol. SEA*, **45**:365-370.*

DROZD, D. 2019. Topographic organization of the pectine neuropils in scorpions: An analysis of chemosensory afferents and the projection pattern in the central nervous system. *Wiesbaden: Springer Spektrum*.

FLEISSNER, G. 1977. Scorpion lateral eyes: Extremely sensitive receptors of Zeitgeber stimuli. *Journal of Comparative Physiology*, **118**:101–108.

FOELIX, R.F. & MULLER-VORHOLT, G. 1983. Fine structure of scorpion sensory organs. II. Pecten sensilla. Br. *Bulletin-British Arachnological Society*, **6** (2):68-74.

GAFFIN, D.D. & WALVOORD, M. E. 2004. Scorpion peg sensilla: are they the same or are they different. *Euscorpius*, **17**:7-15.

GALVIS, W. & FLÓREZ, D.E. 2016. A new telson teratology in the scorpion *Opisthacanthus* Peters, 1861 (Scorpiones: Hormuridae). *Arachnology*, **17**(3):157-158.

GONZALEZ-SPONGA, M.A. 1977. Rectification del caracter ‘‘ojos laterales’’en varios generos de la familia Chactidae (Scorpionida) en Venezuela. *Acta Biologica Venezuelica*, **9**(3):303-315.

GONZALEZ-SPONGA, M.A. 2004. Arácnidos de Venezuela : cincuenta casos de malformaciones en escorpiones (Chactidae, Buthidae, Diplocentridae, Ischnuridae). *Memorias de la Fundación La Salle de Ciencias Naturales*, **157**: 53–67

HEMBREE, D.I., JOHNSON, L.M. & TENWALDE, R.W. 2012. Neoichnology of the desert scorpion *Hadrurus arizonensis*: burrows to biogenic cross lamination. *Palaeontologia Electronica*, **15**(1):10A.

HJELLE, J.T. 1990. Anatomy and morphology. *In* : Polis G. A., eds. *Biology of Scorpions*. *Stanford, CA: Stanford University Press*, 9-63.

IVANOV, V.P. & BALASHOV, Y.S. 1979. The structural and functional organization of the pectine in a scorpion *Buthus eupeus* Koch (Scorpiones, Buthidae) studied by electron microscopy. *Fauna i ekologiya paukoobraznykh. Trudy Zoologicheskogo Instituta (Leningrad)*, **85**, 73-81.

KARATAŞ, A. & KÜRTÜLLÜ, M. 2006. Duplication of pedipalp segments in the scorpion *Androctonus crassicauda* (Olivier, 1807). *Euscorpius*, (**43**):1-4.

KJELLESVIG-WAERING, E. N. 1986. A restudy of the fossil Scorpionida of the world. *Palaeontographica Americana*, **55**:1-287.

KRAPF, D. 1986. Contact chemoreception of prey in hunting scorpions (Arachnida: Scorpiones). *Zoologischer Anzeiger*, **217**(1):119-129.

LEHMANN, T. & MELZER, R.R. 2013. Looking like Limulus? – Retinula axons and visual neuropils of the median and lateral eyes of scorpions. *Frontiers in Zoology*, **10**(1):1-14.

LORIA, S.F. & PRENDINI, L. 2014. Homology of the lateral eyes of Scorpiones: a six-ocellus model. *PLoS One*, **9**(12):e112913.

LOURENÇO, W.R. 2012. The genus *Vietbocap* Lourenço & Pham, 2010 (Scorpiones: Pseudochactidae); proposition of a new subfamily and description of a new species from Laos. *Comptes Rendus Biologies*, **335**(3):232-237.

MANTON, S.M. & HARDING, J.P. 1958. Hydrostatic pressure and leg extension in arthropods, with special reference to arachnids. *Annals Magazine of Natural History*, **1**(3):161-182.

MATTONI, C. I. 2005. Tergal and sexual anomalies in bothriurid scorpions (Scorpiones, Bothriuridae). *Journal of Arachnology*, **33**(2):622-628.

MARTIN-FRIAS, E., DE ARMAS, L. F. & PANIAGUA-SOLIS, J. 2009. *Centruroides gracilis* (Latreille, 1804). Variabilidad de los peines y descripcion de algunas anomalias morfologicas (Scorpiones: Buthidae). *Boletín de la Sociedad Entomológica Aragonesa*, 44: 453–457.*

MELVILLE, J.M. 2000. The pectines of scorpions: analysis of structure and function. Ph. D. Thesis. *Oregon State University*.

MITCHELL, R.W. 1968. *Typhlochactas*, a new genus of eyeless cave scorpion from Mexico (Scorpionida, Chactidae). *Annales de Spéléologie*, **23**(4):753-777.

PRENDINI, L. & WHEELER, W.C. 2005. Scorpion higher phylogeny and classification, taxonomic anarchy, and standards for peer review in online publishing. *Cladistics*, **21**(5):446-494.

ROOT, T.M. & BOWERMAN, R.F. 1981. The scorpion walking leg motor system: muscle fine structure. *Comparative Biochemistry, Physiology Part A: Physiology*, **69**(1):73-78.

SADINE, S.E. 2021. A remarkable bifid aculeus in *Androctonus amoreuxi* (Audouin, 1826) from central Algeria (Scorpiones: Buthidae). *Revista Ibérica de Aracnología*, (38):191-192.

SALABI, F., JAFARI, H. & FOROUZAN, A. 2021. Report of a rare anomaly in the metasoma of *Hottentotta zagrosensis* (Scorpiones: Buthidae). *Iranian Journal of Science, Technology, Transactions A: Science*, **45**:405–408.

SAN-MARTIN, P. & CEKALOVIC, K. 1972. Fijación de los caracteres sistemáticos en los Bothriuridae (Scorpiones). II. Queliceros: estudio de diferenciación a nivel genérico. *Boletín de la Sociedad Biológica de Concepción*, **44**:57-71

SANTIAGO-BLAY J. A. 1986. Morphological malformations among scorpions of Puerto Rico and the adjacent islands. *Pan-Pacific Entomologist*, **62** (1): 77–82

ŠARIĆ, M. & TOMIĆ, J. 2016. The first record of malformed pectines in genus *Euscorpius* (Scorpiones: Euscorpiidae). *Euscorpius*, (**221**):1-10.

SHERWOOD, D. & L. F. DE ARMAS. 2023. On some teratological scorpions in the Natural History Museum, London and checklist of the scorpiological literature on morphological anomalies (Arachnida: Scorpiones). *Euscorpius*, **381**: 1-20.

SCHLIWA, M. & FLEISSNER G. 1980. The lateral eyes of the scorpion, *Androctonus australis*. *Cell and Tissue Research*, **206**, 95–114.

SEITER, M. & TERUEL, R. 2014. Two new cases of metasomal duplication in scorpions, with notes on their reproductive biology (Scorpiones: Buthidae). *Revista Ibérica de Aracnología*, **24**:127-129.

SISSOM, W.D. 1988. *Typhlochactas mitchelli*, a new species of eyeless, montane forest litter scorpion from northeastern Oaxaca, Mexico (Chactidae, Superstitioninae, Typhlochactini). *Journal of Arachnology*, **16**:365-371.

SISSOM, W.D. 1990. Systematics, biogeography and paleontology (64-160 pp). In : Polis G.A. (ed) : Biology of Scorpions. *Stanford, CA: Stanford University Press*

SOLEGLAD, M.E. & FET, V. 2003. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius*, (11):1-56.

STAHNKE, H.L. 1970. Scorpion nomenclature and mensuration. *Entomology news*, **81**(12):297-316.

TATE, A. E., RIDDLE, R. R., SOLEGLAD, M. E & GRAHAM, M. R. 2013. *Pseudouroctonus peccatum*, a new scorpion from the Spring Mountains near "Sin City," Nevada (Scorpiones,Vaejovidae). *ZooKeys* **364**: 29–45.

TERUEL, R. 2003. Nuevos casos de anomalías morfológicas en escorpiones (Scorpiones: Bothriuridae, Buthidae, Chactidae, Chaerilidae, Diplocentridae, Euscorpiidae, Hemiscorpiidae, Ischnuridae, Iuridae, Scorpionidae). *Revista Ibérica de Aracnología*, **7**:235-238.*

TERUEL, R. & REIN, J. O. 2009. On the findings of *Vaejovis mexicanus* C. L. Koch, 1836 and other scorpions in Norway (Scorpiones : Vaejovidae, Euscorpiidae, Hemiscorpiidae). *The Scorpion Files – Occasional Papers*, **2**: 1–3.

TERUEL, R. & BALDAZO-MONSIVAIZ, J.G. 2015. Hermaphroditism, gynandromorphism, and four pectines: an extreme case of developmental anomaly in scorpions (Scorpiones: Vaejovidae). *Euscorpius*, **197**:1-7.

VACHON, M. 1950. Etudes sur les Scorpions. Ill (suite). Description des Scorpions du Nord de l'Afrique. *Archive Institut Pasteur d'Algérie*, **28**:152-216.

VACHON, M. 1957. La régénération appendiculaire chez les scorpions (Arachnides). *Comptes Rendus Hebdomadaires Des Seances de l'Academie Des Sciences* Paris, **244**:2556–2559.

VACHON, M. 1963. De l'utilité, en systématique, d'une nomenclature des dents des chélicères chez les Scorpions. *Bulletin du Muséum national d'Histoire naturelle*, Paris**, 2**:161-166.

VACHON, M. 1974. Etude des caractères utilisés pour classer les familles et les genres de Scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriaux et types de trichobothriotaxie chez les Scorpions. *Bulletin du Muséum national d'Histoire naturelle*, Paris, **104**:857-958.

VOLSCHENK, E. S. & PRENDINI, L. 2008. *Aops oncodactylus*, gen. et sp. nov., the first troglobitic urodacid (Urodacidae : Scorpiones), with a re-assessment of cavernicolous, troglobitic and troglomorphic scorpions. *Invertebrate Systematics*, **22**:235–257. VYAS, A. 1974. The cheliceral muscles of the scorpion *Heterometrus fulvipes. Bulletin Southern California Academy of Sciences*, **73** : 9-14.

WARBURG, M. R. & POLIS, G. A. 1990. Behavioral responses, rhythms, and activity patterns. *In* : Polis, G. A., eds. *Biology of Scorpions*. *Stanford, CA: Stanford University Press*, 224–246.

WARBURG, M. R. 2013. Data mining using multivariate. The circadian rhythm and visual elements in scorpions: A review. *Arthropods*, **2**(4):150–158.

WENDRUFF, A.J., BABCOCK, L.E., WIRKNER, C.S., KLUESSENDORF, J. & MIKULIC, D.G. 2020. A Silurian ancestral scorpion with fossilised internal anatomy illustrating a pathway to arachnid terrestrialisation. *Scientific Reports*, **10**, 14. WATZ, M. & J. A. DUNLOP. 2020. Observations on regeneration of the pedipalp and legs of scorpions. *Euscorpius*, **345**: 1–5

WOLF, H. 2008. The pectine organs of the scorpion, *Vaejovis spinigerus*: Structure and (glomerular) central projections. *Arthropod Structure and Development*, **37**(1):67-80.

WOLF, H. 2017. Scorpions pectines–idiosyncratic chemo-and mechanosensory organs. *Arthropod Structure and Development*, **46**(6):753-764.

YAĞMUR, E.A., KILIÇ, M.S. & YILMAZ, Ö. 2021. An anomaly of chelicera in *Scorpio kruglovi* Birula, 1910 (Scorpiones: Scorpionidae). *Euscorpius*, **335**:1-4.

* Reference vailable at www.sea-entomologia.org