Observations on the Reproductive Structures in Schizodactylus (Schizodactylidae: Orthoptera)

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Abstract

The genus Schizodactylus exhibits highly peculiar characteristics in its social, reproductive, and burrowing behaviors, consistently attracting the attention of entomologists. This study presents detailed morphology of the reproductive structures in Schizodactylus (Orthoptera: Schizodactylidae) with a focus on both male and female reproductive systems. The male reproductive systems contain several specialized structures, such as paired ring-like gonads (testes), malleable vas deferens, epididymis, accessory gland tubules, seminal vesicle, and ejaculatory duct. Each part is well adapted for the production, maturation, storage, and transfer of sperm. Schizodactylus monstrosus studied an extensive network of accessory gland tubules, and this species' accessory gland significantly contributes to increased reproductive performance. The female reproductive system consists of a pair of ovaries with 26–30 ovarioles, paired oviducts, a median genital chamber, and a spermatheca. An ovariole is formed of a terminal filament, a middle egg tube, and a basal pedicle, giving the ovariole a compact, foam-like structure. Progressive oocyte layering of the egg chambers is characteristic, and a muscular calyx at the ovariole base helps move eggs into position for transfer. These structures exhibit complex adaptations in Schizodactylus that enhance its reproductive success. We believe that the present study contributes to a deeper understanding of this ecologically significant and taxonomically distinct orthopteran genus.

Keywords: Schizodactylus, Reproduction, Morphology, Ovarioles, Spermatheca

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Introduction

The genus *Schizodactylus* (Schizodactylidae: Orthoptera) represents a unique group within the order Orthoptera, distinguished by remarkable morphological, behavioral, and ecological traits. Characterized by their rolled wings and fossorial lifestyle, members of this genus are commonly referred to as dune crickets or "monsters." In the local dialect of Larkana, Pakistan, they are known as Pani dharo, a term reflecting their sensitivity to water. The family Schizodactylidae comprises two recognized genera: *Schizodactylus* and *Comicus*, with this distinction first highlighted by Ramme in 1931 following earlier descriptions by Bischoff (1930). *Schizodactylus* species are notable for their large, robust bodies and specialized burrowing adaptations, including powerful mandibles and long antennae used for estimating burrow depth. They exhibit nocturnal, tunnel-building behavior along moist riverbanks such as those of the Indus in Pakistan and the Ganges in India. Notably, *Schizodactylus monstrosus,* also called the Bengal cricket, Bherwa in Bihar, and maize cricket, is distributed across South Asian countries, including Pakistan, India, Bangladesh, Burma, and Sri Lanka. This species typically inhabits sandy, damp soils near water bodies, creating deep burrows for shelter and reproduction. Its population density declines in arid conditions, indicating a preference for humid microhabitats. Despite its ecological importance as a top carnivore feeding predominantly on beetles (Order: Coleoptera) and other orthopterans, *Schizodactylus* remains understudied compared to other orthopteran taxa. Most previous research has focused on taxonomy, morphology, and general ecology, with limited attention to reproductive biology and behavioral ecology. Observations by Khattar (1965, 1966, 1972), Choudhuri et al. (1974), Channa et al. (2011, 2013), Dawwrueng et al. (2018), Sultana (2019), Barkat et al. (2024), and Cigliano et al. (2025) have elaborated on burrow architecture, nymphal development, and sub-social behaviors; however, detailed analyses of mating behavior and reproductive anatomy remain scarce. Early records of *Schizodactylus inexpectatus*, discovered by Martin Holtz in 1897 in the Cilician Taurus Mountains of Turkey, were later revised by Werner and formally placed into the genus *Schizodactylus* by Ramme in 1931. Although once considered extinct in its type locality, subsequent findings in the Çukurova Delta and Alata revived interest in the species; nevertheless, its life history and biology remain poorly documented. In recent field and laboratory investigations (2023–2025), researchers collected over 479 specimens of *S. monstrosus*, *S. minor*, and *Schizodactylus hesperus* Bey-Bienko, 1967 to study morphological differences across developmental stages and to document burrowing and mating behaviors (Table 1). These studies revealed aggressive, cannibalistic mating interactions, particularly among males, and further detailed the progressive nymphal development comprising nine instars over approximately one year. Burrow construction behavior varied with developmental stage, with nymphs and adults excavating tunnels proportionate to their body size, using their antennae to estimate depth. The present study aims to provide a comprehensive analysis of the reproductive structures and behavioral ecology of *Schizodactylus*, emphasizing its anatomical adaptations, mating strategies, and life cycle dynamics. These findings contribute to a deeper understanding of

this ecologically significant and taxonomically distinct orthopteran genus.

Material & Methods

Locality and Sampling Site

The specimens were collected from a small village located near the Khairpur Bridge, Larkana, Sindh, Pakistan (27.4227° N, 68.2835° E). Larkana is situated in the northwestern part of Sindh and is one of the hottest cities in the region, with the highest recorded temperature reaching 53 °C (124.7 °F). It is the 15th largest city in Pakistan by population and is home to the ancient Indus Valley Civilization site, Mohenjo-Daro. The historic Indus River flows south of the city. *Schizodactylus monstrosus* and *S. minor* were collected from the riverbanks of the Indus near Larkana. All collected material was brought to the Entomology Biocontrol Research Lab, Department of Zoology, for further analysis. After examination, the specimens were dissected, and the male and female genital organs were studied.

Dissection procedure

The dissection of *Schizodactylus* was directed mainly to the reproductive organs. The specimen was pinned ventral side up in a dissecting tray using fine pins (Figure 1). A ventral longitudinal incision was gently made, exposing internal anatomy. Under a dissecting microscope, the male and female reproductive structures were identified and studied in detail. The reproductive organs studied were the testes, vas deferens, and seminal vesicles and associated ducts of males and the ovaries, lateral oviducts, common oviduct, and spermatheca of females. Viscera were grossly separated from adjacent viscera, washed with a saline solution, and stored in 70% ethanol for microscopical examination.

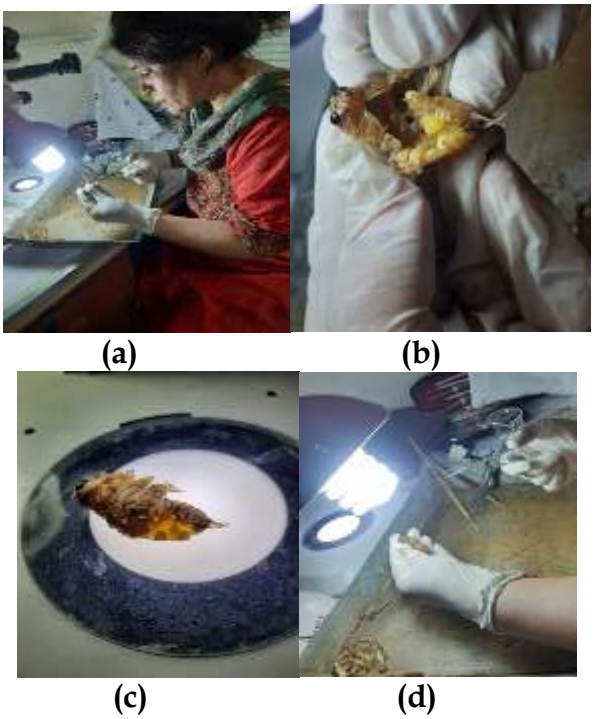

Figure 1. (a-d) Showing dissection of *Schizodactylus*

Results

An examination of *Schizodactylus monstrosus was* performed to assign an appropriate taxonomic status to the insect, which has not been previously able to be determined owing to its morphological and anatomical peculiarities. During this work, the insect's reproductive organs were examined, including some field observations. The details are as follows:

Male Reproductive System of *Schizodactylus*

The male reproductive system of *Schizodactylus* is highly specialized and composed of several interconnected structures responsible for sperm production, maturation, storage, and transfer. Each organ plays a critical role in ensuring reproductive success. Males possess a pair of large, ring-like testes measuring approximately 13–16 mm, enclosed in a protective outer layer. These extend from the metathorax to the 8th abdominal segment. Internally, the testes

contain numerous sperm tubules enclosed in a peritoneal membrane, which facilitates continuous sperm development. Each testis connects to a long, thread-like vas deferens, which serves as the conduit for transporting mature sperm toward the seminal vesicle. As the vas deferens extends through the 4th to 9th abdominal segments, it forms the epididymis—a coiled structure where sperm further mature and acquire motility. The epididymis is connected to several accessory gland tubules, which secrete seminal fluids aiding in sperm transfer and urethral lubrication. In *Schizodactylus monstrosus*, these glands are particularly well-developed. The vas deferens leads to the seminal vesicle, which stores sperm encapsulated in spermatophores. Finally, the thick-walled ejaculatory duct serves as the terminal conduit, expelling sperm during copulation.

Female Reproductive System of *Schizodactylus*

The female reproductive system comprises a pair of ovaries, paired lateral oviducts, a median genital chamber, and a spermatheca. Each ovary consists of approximately 26 to 30 ovarioles, each about 26–30 μm long, collectively forming a foam-like cluster. Each ovariole connects directly to the oviduct, the site of fertilization. Structurally, each ovariole is divided into three regions: (1) the terminal filament, a slender anterior extension; (2) the middle egg tube, containing eggs at varying developmental stages; and (3) the basal pedicle, providing structural support. The terminal filaments of all ovarioles converge to form the ovary's framework. The egg tube contains several follicles arranged sequentially, with posterior oocytes typically more developed. At the junction of the ovarioles and oviduct lies the muscular calyx, which facilitates the movement of mature eggs into the oviduct. The spermatheca, located within the genital chamber, stores sperm received from the male, enabling internal fertilization.

Field observation

Recent field studies have revealed key behavioral patterns of *Schizodactylus monstrosus*, particularly through nocturnal collections conducted between 2:00 AM and 5:00 AM and daytime burrow excavation activities. These temporal differences in activity suggest a strong nocturnal tendency in the species, likely linked to predator avoidance and environmental conditions such as temperature and humidity. The release of collected specimens into their natural habitat and subsequent observation of their burrowing behavior provided valuable ecological insights. The burrow construction, depth, and orientation reflect adaptive strategies for thermoregulation, moisture retention, and protection from predators. Such behaviors emphasize the species' specialized ecological niche within sandy and arid habitats. The findings underscore the importance of conserving *Schizodactylus monstrosus*, not only due to its unique behavioral and ecological traits but also because of its role in maintaining ecological balance within its native ecosystem. Habitat disturbance and environmental changes pose significant threats to its survival. Therefore, focused conservation efforts are essential to preserve this ecologically significant species.

Table 1: Showing a collection of different species of genus *Schizodactylus* from Larkana.

Species Name	Total Specimens	Mean ± SE	Collection site	Collection Period
Male Population				
S.monstrous	80	4 ± 0.40	Larkana	2023-2025

S.minor	39	1.95 ± 0.49	Larkana	2023-2025
S. hesperus	8	0.72 ± 0.69	Larkana	2023-2025
Female Population				
S.monstrous	107	5.35 ± 0.84	Larkana	2023-2025
S.minor	48	2.4 ± 0.516	Larkana	2023-2025
S.hesperus	13	1.18 ± 0.56	Larkana	2023-2025
Nymph population				
S.monstrous	118	5.9 ± 1.008	Larkana	2023-2025
S.minor	52	2.6 ± 0.49	Larkana	2023-2025
S,.hesperus	14	1.27 ± 0.532	Larkana	2023-2025

The three species of *Schizodactylus* collected from Larkana included *S. monstrosus*, which was historically the most abundant species at all life stages, 80 males, 107 females, and 118 nymphs in our sampling, indicating that it is probably the dominant species in this region. *S. minor* was the second most abundant species, while *S. hesperus* had the least number of specimens collected (male specimens were few, at just 8). A slight female bias was observed across species, most notably *S. monstrosus*. The nymph populations of each of the three closely matched the adult counts, indicating a consistent and active reproductive cycle within the habitat. Consistent with its stable and largest population, *S. monstrosus* had the highest mean and standard error values across categories. In contrast, *S. hesperus* remained at a low abundance with relatively stable SE values (0.72 ± 0.69), and it may be indicative of an only more localised and limited distribution in the region.

Discussion

As far as a thorough anatomical and comparative study of the reproductive structures of Schizodactylus *monstrosus* is concerned, the work of Khattar (1966) is very informative, and it clearly distinguishes some of the morphological modifications which differentiate this species from the other orthopterans. Males also possess relatively overdeveloped testes (~14 mm long), a sparsely coiled epididymis, and an array of five morphologically diverse accessory gland tubules that presumably play many secretory roles in sperm maintenance and copulation. Notably, there is a lack of ejaculatory vesicles, which are thought to be a diagnostic character for the superfamily Tettigonioidea (Snodgrass, 1937; Imms, 1957), and while seminal vesicles are present, this is a condition more reminiscent of primitive assemblages in groups with Blatidae, Mantidae and Gryllotalpa (Ito, 1924; Albrecht, 1953, 1956). For the females, the reproductive system is characterized by the lack of a median oviduct and a well-developed muscular calyx in the base of the ovarioles, a feature not commonly observed in Tettigonioidea but described for Acrididæ (*Dissosteira carolina*; Snodgrass, 1935). Spermatheca bifid, with an elongated, coiled duct and with separate storage and accessory portions. The muscular system of the genitals shows specialisations too. In the seventh abdominal segment, the inner sternal muscles do not insert on the eighth sternum as they do in most Orthoptera (Ford, 1923) but on chitinous sclerites of the genital chamber, thus supporting the oviducts and also adducting the genital chamber. In the same way that the sternum is simplified in the eighth configuration, the muscle of the eighth sternum is reduced

in the absence of the ovipositor — a modification attributed to their subterranean habitus (Khattar, 1965) but functional in supporting the oviducts. All muscle and reproductive modifications examined collectively suggest that *S. monstrosus* occupies an intermediate position in Orthoptera concerning several characters and emphasizes its phylogenetic and taxonomic importance in Saltatoria. Our results on the reproductive anatomy of *Schizodactylus* concurred in several important respects with those given by Khattar (1966), while also providing some new refinements and additional detail. In both studies, the male testes are a massive structure filled with a large number of sperm tubules and enclosed in a peritoneal membrane, and spiralled epididymis segments are formed in the vas deferens extending through the abdominal segments. Our description, however, highlights the ring-like structure of the testes (13–16 mm), whereas Khattar measured them flat and broad (~14 mm × 6 mm), which is marginally different. The current results further outline the spermatophore filling aspect of the seminal vesicle, which was only touched upon by Khattar in this work, as his attention was mostly directed towards the anatomical arrangement. Moreover, whilst their roles are generally classified as those of seminal fluid secretion in our account due to significant development of accessory gland tubules in the observed stage, in Khattar's version, they were grouped into five types based on structure and possible secretory roles. On the female side, present findings reconfirm the number of ovarioles (26–30), presence of a calyx, and gross structure of each ovariole into terminal filament, egg tube, and pedicle, which closely matches that of Khattar. We, however, provide more accurate measurements (e.g. ovariole length) and emphasize the foam-like organization of ovarioles and calyx musculature — features that were not emphasized in the original study. Both studies show that the spermatheca is used to store sperm, however, the study uses a simplified structure of a single spherical spermatheca, while Khattar gives an extensive bifid spermatheca with a long-coiled duct. Overall, ongoing work is unpacking and updating Khattar's nascent anatomy, validating many of his conclusions but bringing new morphological depth and functional insight. Besides this population dynamics of *Schizodactylus* species show that *S. monstrosus* is the predominant species of the Larkana. These relatively high and uniform counts in male, female, and nymph populations of the species indicate that this species is well adapted to the environmental conditions of the study area. A balanced sex ratio and presence of nymphs hint at a healthy and reproducing population. Conversely, *S. hesperus* does not seem to be as ubiquitous, and may be more specialized or environmentally constrained. But the presence of all three life stages, however, confirms it continues to reproduce in the area. Such distribution patterns help understand ecological dynamics and potential conservation needs of lesser-represented species like *S. hesperus.*

Conclusion

The findings of the current study support and extend earlier findings of Khattar (1966), including important anatomical features such as enlarged testes, coiled epididymis, absent ejaculatory vesicles, bifid spermatheca/vesicular, and specializations of the musculature. It includes refinements to anatomical detail, such as more precise measurements, structural nuances (e.g., ring-shaped testes and foam-like calyx organization), and

functional interpretations of glandular secretions. Such findings not only contribute to our knowledge of *S. monstrosus* reproductive morphology but also highlight its degree of evolutionary significance in *Saltatoria* phylogeny.

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