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A Comparative Study on the Fine Structure of Flight Muscle of Mature Male and Female *Poekilocerus bufonius* Klug (Orthoptera Pyrogomorphidae)

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ABSTRACT. The shape and size of the flight muscles fibres of male *P. bufonius* are almost uniform. The nucleus is situated at the periphery of the fibre and contains normal distribution of the chromatin. The myofibrils are in almost perfect transverse register, with regular Z and I bands. The mitochondria are moderate and contain very well developed cristae. The sarcoplasmic reticulum and its association with T-system to form dyads are well developed.

In contrast, the female flight muscle fibres are reduced in size to slender thread-like structures. The decrease in width is due to atrophy of myofibrils so, that the surface (sarcolemma) becomes scalloped or markedly irregular. The nuclei are located peripherally and are surrounded by undifferentiated sarcoplasm, suggesting nucleus shrinkage (Pyknosis). The pyknotic nuclear chromatin is aggregated or climped into numerous masses occasionally adjacent to the nuclear membrane. The myofibrils are small and the cross-striations are poorly defined. The Z-bands are irregularly arranged, or absent in some cases. Less organized myofibrils and indistinct sarcomere bands are evident. The mitochondria are scarce and the sarcoplasmic reticulum is abundant with clear indication of dilation. More study is needed to ascertain whether atrophy of flight muscle of mature adult female coincides with gonad growth or the flight muscle never develop.

Introduction

It has been reported[1], that insects which have secondarily lost the ability to fly lack two fundamental biochemical characteristics present in those which have regained

this ability; a marked increase in extramitochondrial glycero-p-dehydrogenase activity after the last ecdysis and a virtual absence of lactate dehydrogenase. Huddart and Oates[2] studied the fine structure of stick insect (flightless) and locust skeletal muscle and found that it has a much more extensive sarcoplasmic reticulum and more frequent dyads per unit area of section than that of stick insect muscle.

Physiological studies of excitation contraction coupling on insect flight muscle[3,4,5,6,7] have shown that the physiological activity of synchronous insect skeletal muscle is similar to that of other striated muscle, including vertebrates.

Concerning insect flight muscle, Finlayson[8] reported that the older literature contains many descriptions of the histological events accompanying the degeneration and disappearance of muscle, but there are only a few accounts in which electron microscopy has been used (at least in insect flight muscle).

The grasshopper, *Poekilocerus bufonius,* is found in all provinces of Saudi Arabia. This species in nature probably feeds exclusively on asclepiad plants[9] one of which is *Calotropis procera. Poekilocerus bufonius* is characterized by the ability to consume *C. procera*[10] which contains toxic cardiac glycosides (CGs). The latter are specific inhibitor to Na^+/K^+-ATPase activity and minute of CGs is said to cause death to most vertebrates and invertebrates[11,12,13], however, Al-Robai *et al.*[14] reported the presence of ouabain-resistant Na^+/K^+-transporting ATPase in the membrane microsomal preparation from Malpighian tubules and hind-gut of *P. bufonius.*

Poekilocerus bufonius ingest and sequester CGs into their tissues and bilobed gland and use them for protection from predators[9,10,15], it is possible, therefore, that the species utilizing a toxic chemical may suffers physiological cost or place stress on their bearers[16].

Flight muscle is, obviously, essential for flight. The mature adult female of *P. bufonius,* is incapable of flight or wing fluttering. In contrast, the male of this species can fly for a very short distance. In view of the importance of the contribution of insect flight muscle component in the ability of the insect to perform flight, it might be possible to observe an ultra structural variation between the flight muscle of female (Disuse) and that of the male.

The present study was undertaken to investigate to what extent the flight muscle component varies between mature male and female *P. bufonius.* The results may help in extending our knowledge on the relationship between structure and function of muscle.

Material and Methods

Male and female grasshoppers, *P. bufonius,* were collected from King Abdulaziz University (KAU) campus, Jeddah, Saudi Arabia. They were maintained in a large cage in open air conditions and supplied daily with fresh branches of *C. procera.*

The gut of mature adult *P. bufonius* gravid females and males (four of each) was removed by disrupting the "Neck membrane", severing the posterior tip of the abdo-

men and withdrawing the gut attached to the head. The thorax was then cut open ventrally and pinned out on a cork board, prior to the applications of ice-cold (0-4°C), fixative, 2.5% glutaraldehyde in 0.1 M sodium cacodylate buffer (pH 7.3) and containing 0.32 M sucrose on the flight muscles. Postifixation was conducted for 2 hours by immersing the tissues in ice cold 1% Osmium tetroxide maintained at pH 7.3 with cacodylate buffer, dehydrated in acetone and embedded in Epon 812. Thick sections (1 μm) were stained with toluidine blue, whereas thin sections were stained with lead citrate and uranyl acetate[17] for 30 min. prior to their examination with Jeol 100 CX TEM.

Samples for scanning electron microscopy (SEM), were fixed in 2.4% glutaraldehyde as described above, dehydrated in an ascending series of ethanol and critical point dried. The muscles were coated by gold-palladium after carbon coating then viewed and photographed using a Jeol SEM-35.

Results

The mature adults female grasshopper, *P. bufonius,* are incapable of flight. The flight muscles of mature adult females are very small and reduced to slender thread-like structures. They are characteristically pale in appearance. In contrast, the male flight muscles are relatively large and are of reddish-brown colour.

Using the scanning electron microscope, the surface of the flight muscle fibres of male and female *P. bufonius,* showed regular transverse striations (Figs. 1 and 2). These striations are presumably due to local shrinkage at the Z-band level. The nuclei are clearly seen under the sarcolemma at the muscle fibre periphery (Fig. 1). In

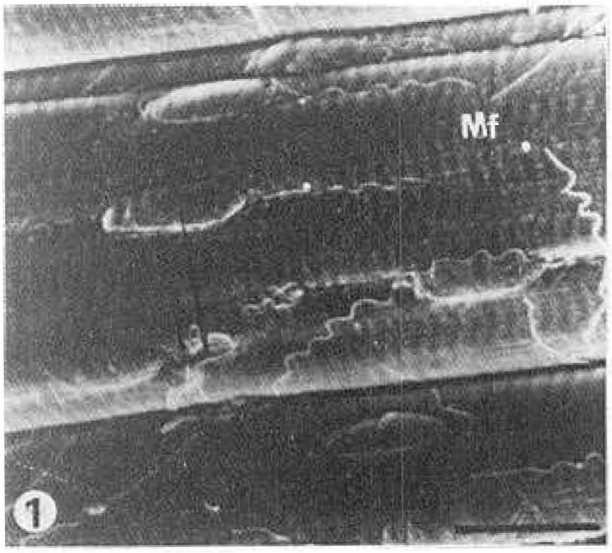

FIG. Scanning electron micrograph (SEM) of male flight muscle fibres to show the regular transverse striations and the presence of nucleus in peripheral position (arrows). MF: Muscle fibres. Scale 10 μm.

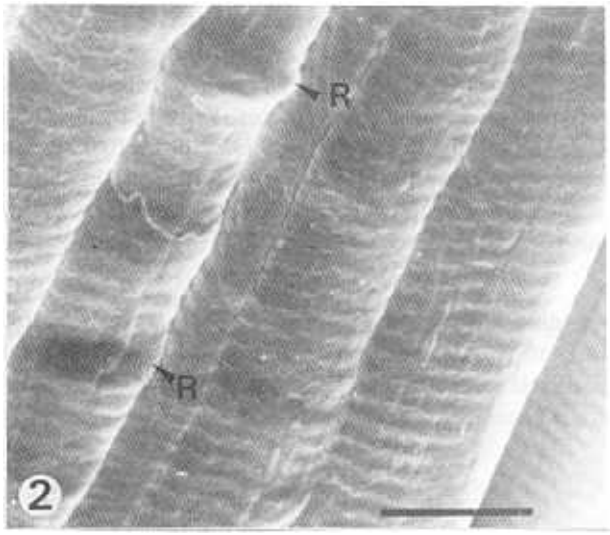

FIG. 2. SEM of female flight muscle fibres. Note the shrinkage and decrease in the width of some muscle fibres (upper left). R: Ridge. Scale 10 μm.

contrast to male muscle fibres, some of the female muscle fibres suggest a decrease in their width. This decrease in with leads to shrinkage of sarcolemma as demonstrated by ridges along the muscle fibres (Fig. 2). Examination of transverse sections of male flight muscle by light and scanning electron microscope demonstrated muscle fibres of compact arrangement, normal shape and size (Fig. 3). In contrast, transverse sections of female flight muscle shows numerous spaces between the muscle fibres (Fig. 4).

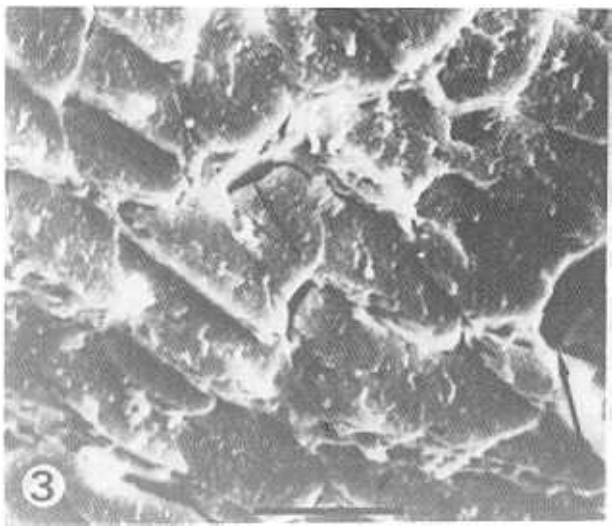

FIG. 3. SEM of transverse section through male flight muscle. Few space (arrows) is present between myofibrils. Scale 8 μm.

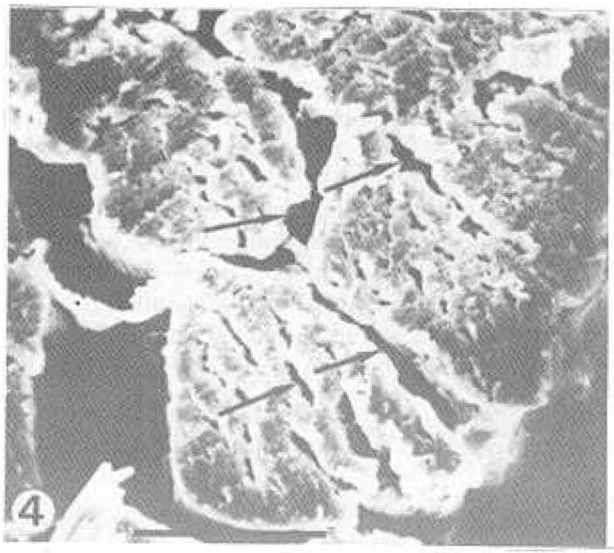

FIG. 4. SEM of transverse section through muscle fibres of female flight muscle. Numerous space between muscle fibres (Arrows) are shown. Scale 2 μm.

Examination of transverse sections through median dorsal longitudinal indirect flight muscle of male *P. bufonius* shows considerable variation of the shape and size of each individual fibre profile (Fig. 5). However, the peripheral fibres tend to be similar in shape and size (Fig. 5).

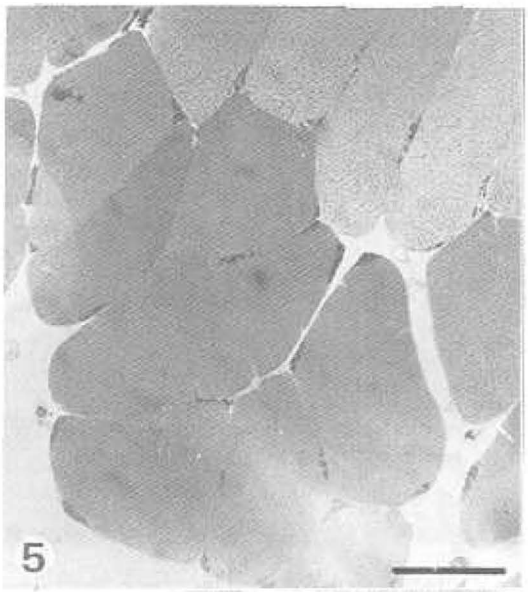

FIG. 5. Transverse section through part of the median dorsal longitudinal flight muscle of male. Note the peripheral position of the nuclei, the shape and size of muscle fibres. Scale 10 μm.

In longitudinal sections of male flight muscle, the myofibrils are usually in almost perfect transverse register, as indicated by the relatively straight rows of Z-bands (Fig. 6). However, the disturbance of some sarcomeres, seen in the section may be due to the preparation. The sarcomeres exhibit the band pattern typical of insect flight muscle[18]. Distinctive I-bands can be seen on either side of the Z-band (Figs. 6 and 7) and most of the sarcomere length being represented by the A-band. Tracheoles are abundant in the male flight muscles (Figs. 6 and 8). There is a considerable variation in the shape of the myofibrillar profiles as seen in transverse sections (Figs. 8, 9 and 11). The shapes range from more or less circular to oblong or oval profiles. The thin (actin) and thick (myosin) myofilaments can be seen clearly in the transverse section of the myofibrils (Figs. 8 and 10). The mitochondria are moderate, but they contain a large number of compact cristae (Figs. 7, 8 and 10).

The sarcoplasmic reticulum (Figs. 6 and 10), and its association with the T-system (Dyads) (Fig. 8) is clearly seen. The distribution of the sarcoplasmic reticulum over

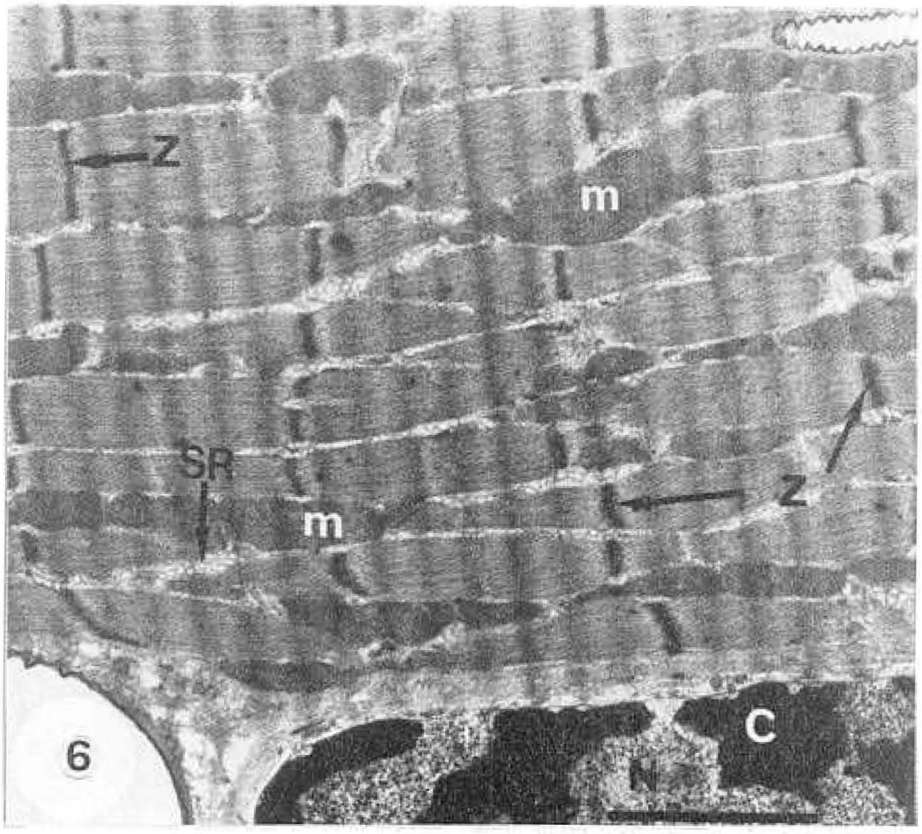

FIG. 6. TE micrograph of longitudinal section through the muscle fibre of male flight muscle to show clearly defined cross-striations, regularity of z-bands (z) and the peripheral position of the nucleus (N). tr: tracheole; m: mitochondria; C: chromatin. Scale 2.5 μm.

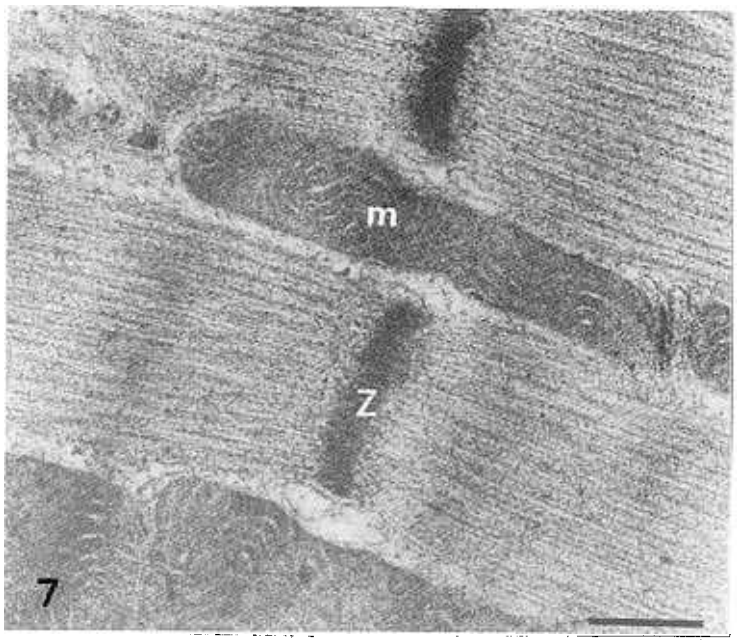

FIG. 7. TEM of longitudinal section through male flight muscle fibre. Regular z-band (Z) is clearly seen. m: mitochondria. Scale 0.5 μm.

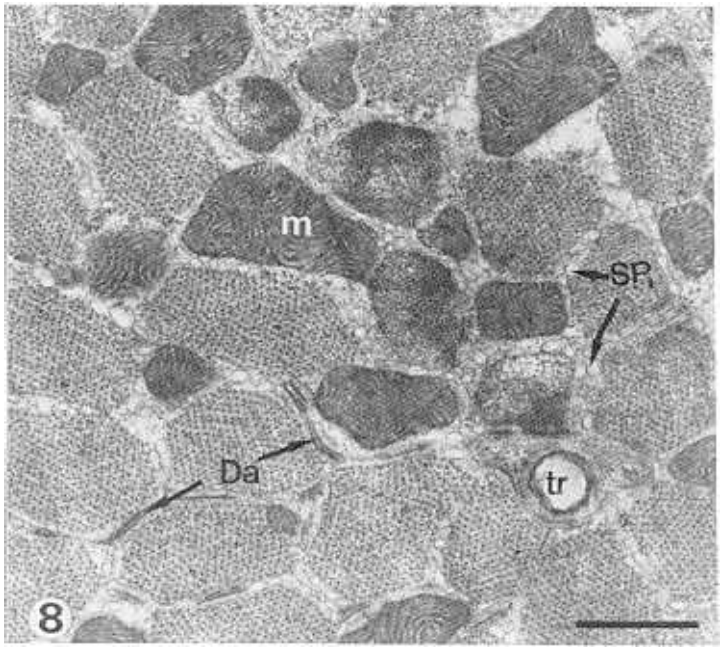

FIG. 8. TEM of transverse section through the muscle fibre of male flight muscle. m: mitochondria; Da: dyad; tr: tracheole; SR: sarcoplasmic reticulum. Scale 1 μm.

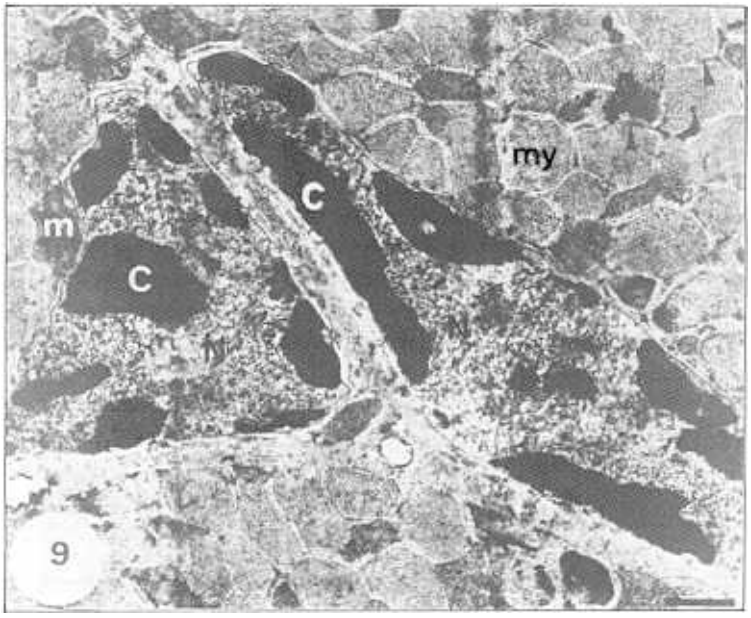

FIG. 9. TEM of transverse section through flight muscle showing the peripheral position of nuclei (N) and the arrangement of myofibrils (my) within the muscle fibre. Notice the moderate number of mitochondria (m) and dyad (arrow heads). C: chromatin. Scale 1 μm.

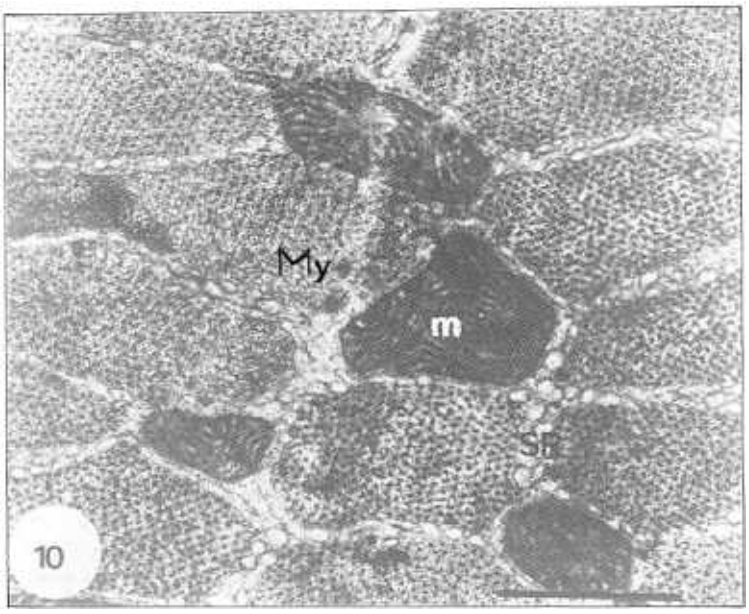

FIG. 10. A transverse section through muscle fibre of male flight muscle. Note the shape, size and arrangement of myofibrils (My). m: mitochondria; SR: sarcoplasmic reticulum. Scale 0.5 μm.

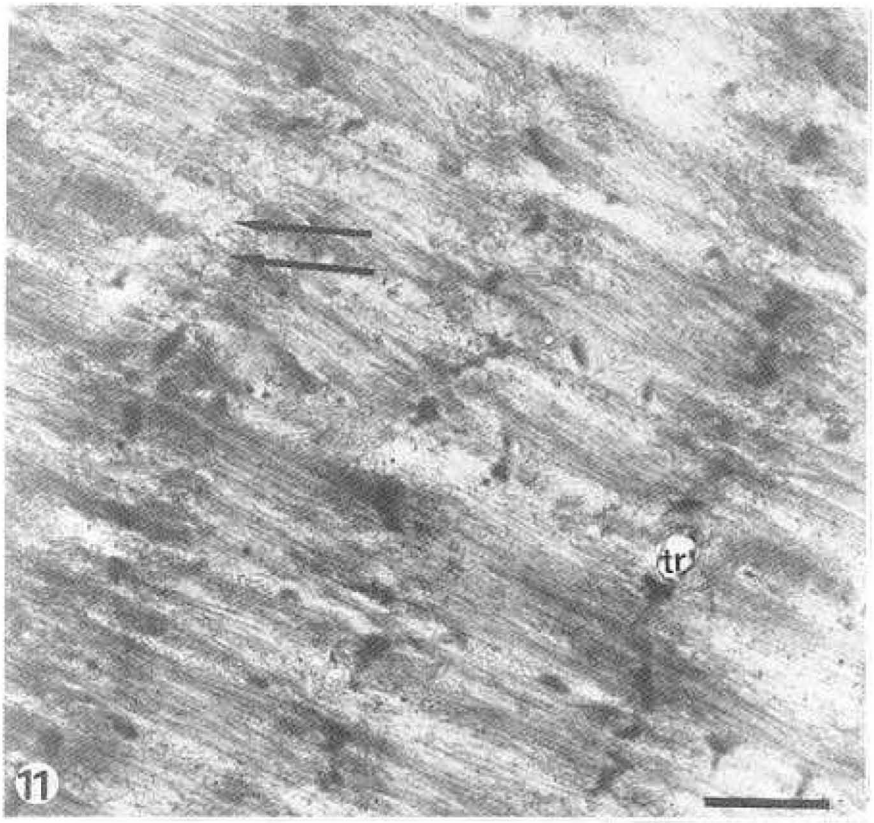

FIG. 11. A longitudinal section through female flight muscle fibre. Observe the reduced size of myofibrils, the poor striation, the irregular shape of z-band and the absence of some z-bands (arrows), tr: tracheole. Scale 1 μm.

the myofibrillar surface and the separation between the adjacent myofibrils and the associated mitochondria is also demonstrated (Figs. 8 and 10).

The size of myofibrils is very small in female flight muscle (Fig. 11), compared with that in male (Fig. 6). The nuclear chromatin is aggregated or clumped into numerous masses adjacent to the membrane (Fig. 12). Occasionally, some nuclei contain fragmented chromatin and careful examination shows that the nucleus is surrounded with undifferentiated sarcoplasm (Fig. 13). In contrast to the banded pattern of male flight muscle (Figs. 6 and 7), the cross-striations of female flight muscle are poorly defined and the Z-bands were irregularly arranged. (Figs. 11, 14, 15 and 16).

Less organized myofibrils (Fig. 12) and indistinctive sarcomere bands of the female flight muscle fibres (Figs. 14, 15 and 17) are evident. In some cases the Z-bands were not seen (Fig. 11) and in others the myofilaments are absent from some sarcomeres (Fig. 16). Fragmented myofilaments are widespread in female muscle (Figs. 14, 17 and 18).

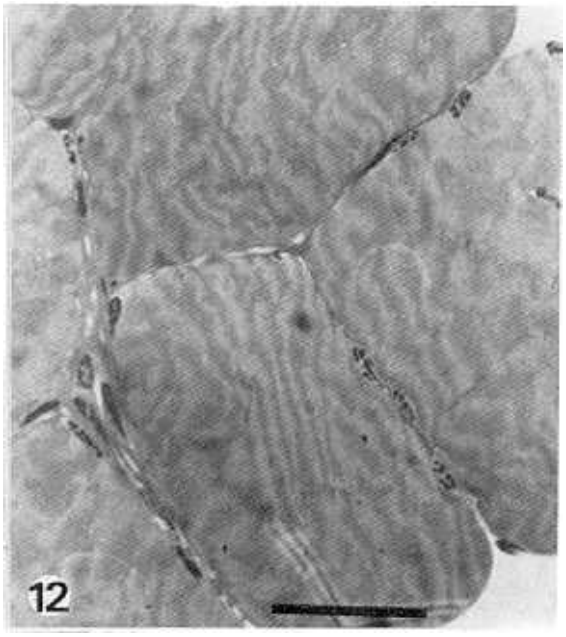

FIG. 12. Transverse section of female flight muscle fibres. Wavy appearance of the component of fibres is evident. Scale 10 μm.

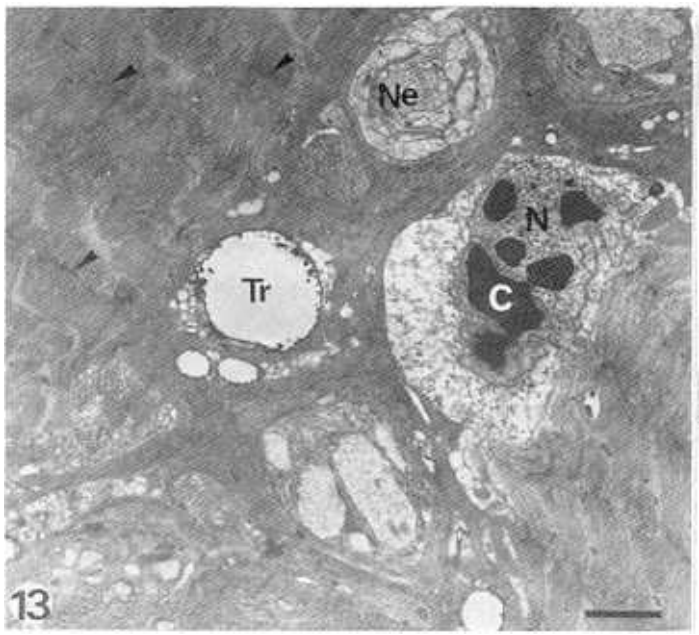

FIG. 13. A longitudinal section through female flight muscle fibre showing distorted z-band (arrow heads). Note the presence of intact nerve (Ne) and nucleus (N) surrounded by undifferentiated sarcoplasm. Tr: trachea; C: chromatin. Scale 1.44 μm.

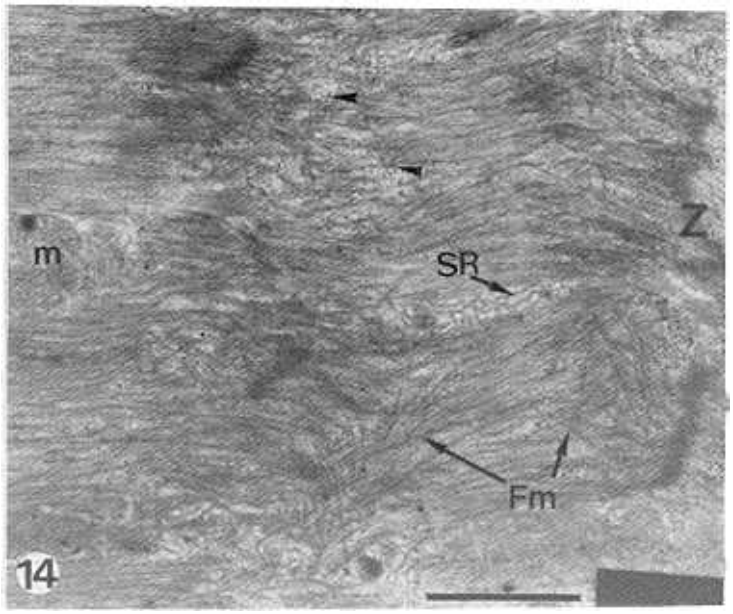

FIG. 14. TEM of longitudinal section through female flight muscle fibre. Note the dilation of sarcoplasmic reticulum (SR), particles of glycogen (arrow heads), the irregular z-band (Z) and fragmented myofilaments (FM). Scale 1 μm.

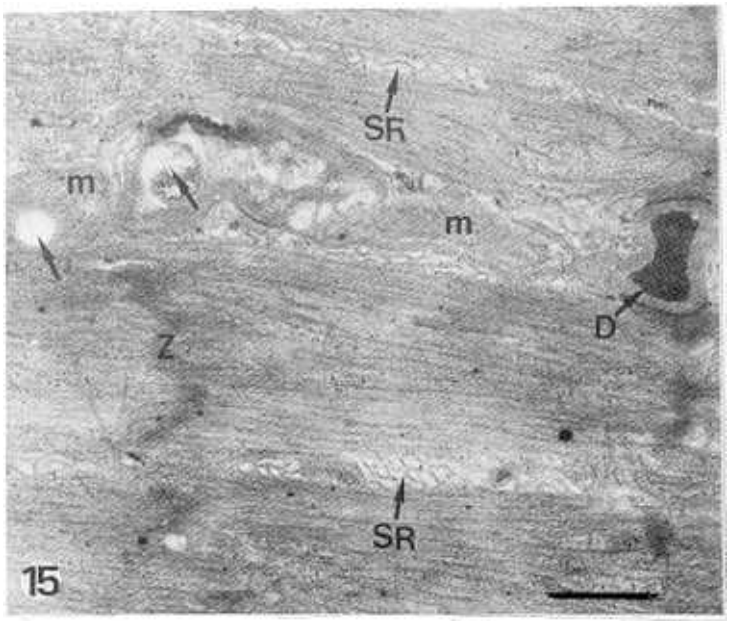

FIG. 15. A longitudinal section through female flight muscle fibre. Note the presence of vaculated mitochondria (arrows), M: mitochondria; SR: sarcoplasmic reticulum; Z: z-band; D: membrane bound electron dense body. Scale 1 μm.

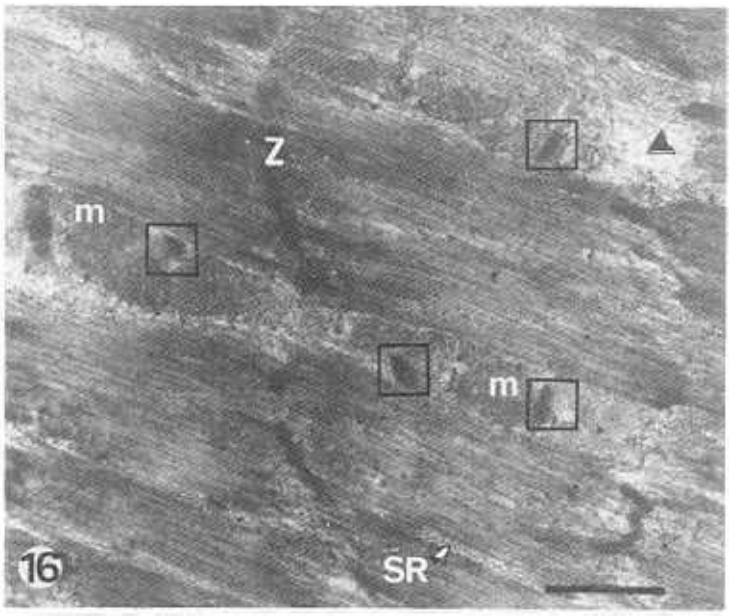

FIG. 16. A longitudinal section through female flight muscle of *P. bufonius*. Note the absence of part of sarcomere (triangle) and the presence of membrane bound dense bodies (squares). m: mitochondria; SR: sarcoplasmic reticulum. Scale 1 μm.

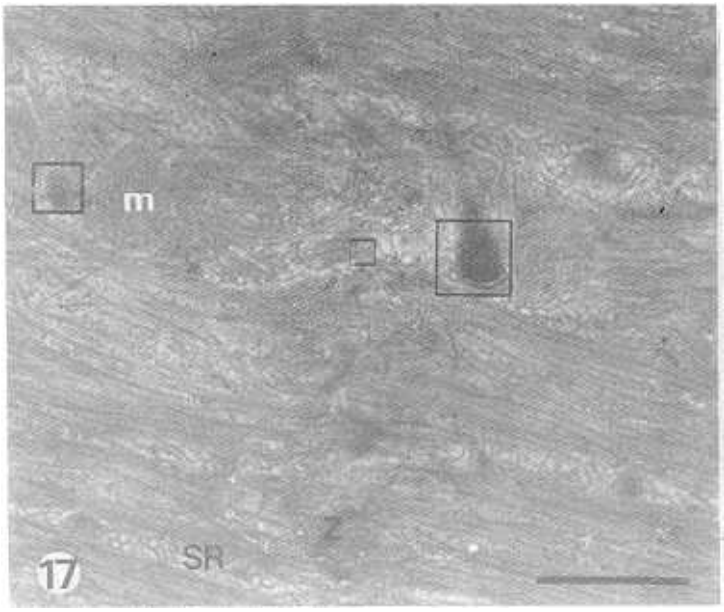

FIG. 17. A longitudinal section through female flight muscle fibre. Note the presence of small membrane bound dense body (small square) and large membrane bound dense body (large square). m: mitochondria; SR: sarcoplasmic reticulum. Scale 1 μm.

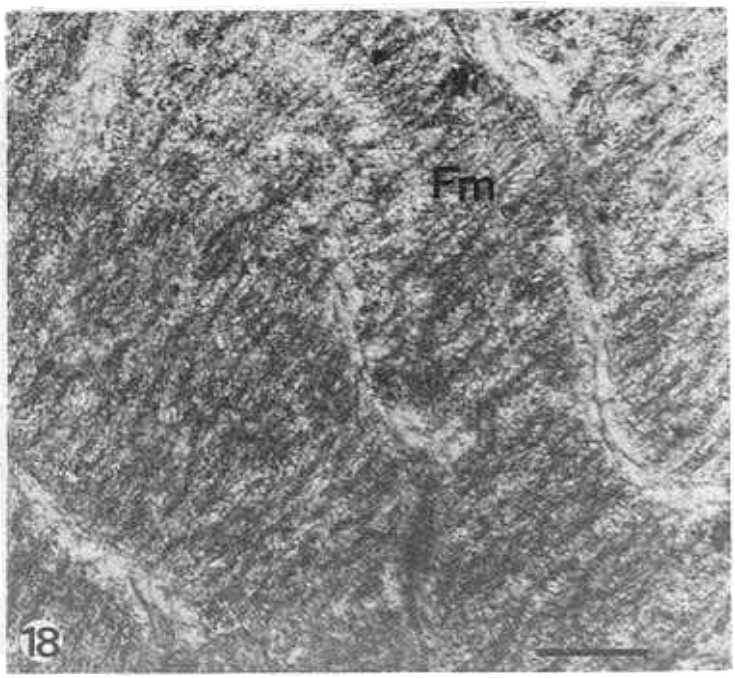

FIG. 18. A transverse section through muscle fibre of female flight muscle. Note the fragmented and distorted myofibril (Fm), in which neither thick nor thin filaments can be seen. Scale 0.3 μm.

The mitochondria are scarce in female flight muscle (Figs. 15 and 16). Occasionally, vacuolated mitochondria are observed (Fig. 15). However, apart from the vacuolation of a limited number of mitochondria, they contain dense cristae (Figs. 16 and 17), which is similar to that of male (Figs. 8 and 16). Well developed sarcoplasmic reticulum is present (Figs. 14, 15, 16 and 17). However, prominent dilation of sarcoplasmic reticulum is a general characteristic of female flight muscle. Membrane found electron dense bodies of different sizes were encountered adjacent to the mitochondria (Fig. 15) and between myofibrils of female flight muscle (Figs. 16 and 17). Very few tracheoles and nerve fibres are also present (Figs. 11 and 13).

Discussion

The observation presented in this study suggest a very severe atrophy of the flight muscle; the flight muscle fibres being very small and thread-like structures. This is due to the reduction in the number and size of the myofibrils on the peripheral region of the muscle fibre, so that the surface becomes scalloped or markedly irregular. Similar observations have been reported for the flightless grasshopper *Romalea microptera*[19]. The flight muscles of female *P. bufonius* are characteristically pale in appearance. In contrast, the mature adult male of this grasshopper is small, light bodied and the wings are relatively large. The flight muscles are reddish-brown in

colour. Similar results have been reported for male locusta migratoria[18]. However, although the male *P. bufonius* is not a good flier, it can still flutter the wings and fly for a short distance. The possible significance of differences in muscle colour was indicated by the studies of Usherwood[20]. He indicated that the "White" muscle fatigue more rapidly than the "Red". In addition, the "Red fibre" has higher levels of succinic dehydrogenase, correlated with a large volume of mitochondria[21]. The latter are scarce in female flight muscle.

The flight muscle of the female showed poorly defined cross-striation and Z-bands are distorted and irregularly arranged. Mitochondria are scarce and apart from vaculation of a limited number of mitochondria, they are similar in appearance to that of the male. The sacroplasmic reticulum is well developed and dilation is a general characteristic and this may explain the presence of spaces between the muscle fibres of female. The above observation corresponds with that reported in other insects[8] and vertebrate skeletal muscle including human[22, 23 and 24] Wasting syndromes that occur in senility, nutritional deficiencies and prolong chronic infections often result in diffuse atrophy of skeletal muscle[25]. The main features that can be recognized are reduction in volume, loss of striation, disturbance of fibrillar structure, nuclear pyknosis and disintegration of myofilaments. Ghadially[24] reported that a consequence of such loss of myofibrils, there is relative abundance of intervening sarcoplasm structures, such as mitochondria, triads (Sarcoplasmic reticulum in the present study), and glycogen particles.

Degeneration and atrophy of muscle have been observed in a variety of experimental and pathological diseases, but none of the ultrastructural alterations are specific for each given disease[22, 23, 24]. This may suggest that whatever the causes of muscle degeneration and atrophy, the process is similar. However, Wyllie[26] has classified cell death into is "necrosis", which occurs exclusively in circumstances of wide departure from physiological conditions, and "apoptosis", which occurs in normal tissue turnover, embryogenesis, metamorphoses and endocrine depended tissue atrophy.

Concerning the atrophy of female *P. bufonius* flight muscle, which occurs in normal female loaded with eggs, it is tempting to suggest that "apoptosis" is the mechanism utilized during muscle atrophy. However, the cause of atrophy is difficult to assign to disuse in a mature adult or to retrenchment. The two physiological situations are often interchanged, compared and confused in literature[8]. Lockshin[27] reported that muscle tissue in vertebrate and invertebrate serves as a protein reservoir, a large percentage of which is labile and readily subjected to degradation under conditions of starvation, disuse or loss of innervation[28, 29]. Scudder[30] discussed the degeneration of flight muscle in detail and throws doubt about the possible physiological link between flight muscle and egg production. He demonstrated that the smaller flight muscle in flightless form of *Cenocorixa bifida* are a consequence of retarded growth, not degeneration. It is well known that in some insects, after mating and dispersal flight has taken place, flight muscles are no longer required and are utilized as a food reserve or provide a significant quantity of protein for the production of eggs[8]. Edwards[31], reported that degeneration of the indirect flight muscle in

adult female of *Dysdercus intermenius* coincides with oocyte growth and is under endocrine control. Chesky[32] reported that locomotion (and probably flight) is a process animals developed for the purpose of mating seeking food, or escaping from hostile environmental conditions. It is possible that the female (usually have the tendency to a shorter winged condition), and male of *P. bufonius*, which used to occupy and have developed a mechanism to repell predators[10], need no flight. Popov and Kevan[33] reported that members of the genus Poekilocerus generally move, let alone travel, little during course of their lives. However, the males are capable of flights facilitating encounters between the sexes[33]. In fact, Euw *et al.*[9], have reported that *P. bufonius* has many separate line of defence apart from its warning coloration, (1) the ejection of a jet of foam for defensive fluid containing cardenolides and histamine (each insect contained about one cat lethal dose); (2) a penetrating and disagreeable odour, which can be perceived by a human observer from a distance of several meters; (3) toxic cardenolides in the tissues of the body. It is possible, therefore, that the atrophy of the female flight muscle of *P. bufonius* promotes reproduction by diverting amino acids to the egg formation. There is normally little displacement between food/shelter and oviposition habitats, that is, during the period in the life of a species when the furthest displacements might be expected. Trump *et al.*[34], indicated that the death of the organ is of vital importance in biology because they occur as normal part of the economy of every organism even during development.

It has been recognized that denervation of muscle leads to atrophy and eventually the degeneration of the muscle fibres. However, Goldspink[35], indicated that it was not clear whether the atrophy and degeneration was due to the changes in activity of the muscle or whether the nerve produces substances or in some other way imports stability to the muscle fibres. Richards and Davies[36], reported that degeneration of the flight muscles occurs after sexual maturity in many species, where the process promotes reproduction by releasing amino acids that can be used in egg formation. The alate forms of *Brevicoryne brassicae, Myzus pericae, Aphis fabae* and other aphids undergo flight muscle degeneration (histolysis) after settling on their host plant and are caused by hormonal changes[37, 38]. A similar process is also found among scolytid beetles in which, after moving to a new tree, the male and female do not fly and their flight muscle is reduced to functionless ribbons[39, 40]. Whether the atrophy of flight muscle of mature adult female of *P. bufonius* coincides with oocyte growth, the muscle never develop (developmental atrophy), due to physiological cost affected by toxic GC or interreaction between GC and endocrine factors, remains to be established.

Acknowledgement

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دراسة مقارنة للتركيب الدقيق لعضلات الطيران في ذكر وأنثى *Poekilocerus bufonius* البالغة (مستقيمات الأجنحة ، بيروجومورفيدي)

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المستخلص . أشكال وأحجام الألياف العضلية لعضلات طيران ذكر بوكيلوسيرس بوفونيس متشابهة وتوجد الأنوية في الجهة الطرفية لكل ليفة عضلية وتمتاز بتوزيع الكروماتين والتصاقه بالغشاء النووي الداخلي . الليفات العضلية منتظمة التخطيط كما يظهر ذلك من الانتظام المتوازي لشريط (Z) ووضوح شريط (I) ، أعداد الميتوكوندريا متوسطة ولكنها تحتوى على أعراف كثيفة ومتطورة . الشبكة الساركوبلازمية واتصالها مع نظام (T) لتكوين الثنائي (Dyad) متطورة أيضًا .

بالمقارنة فإن ألياف عضلات الطيران لأنثى بوكيلوسيرس بوفونيس بيضاء وحجمها مختزل إلى تراكيب خيطية ، ويعزى الاختزال في عرض الليفات العضلية إلى انكماش الليفات العضلية ولذلك فإن الغشاء المحيط بالليفة العضلية به نتوءات غير منتظمة . تقع الأنوية في الجهة الطرفية لكل ليفة عضلية وتحاط بجزء من سيتوبلازم الخلية غير متميز ويشر هذا إلى انكماشها (بيكنوسس) والكروماتين متجمع في كتل كبيرة بالقرب من الغشاء النووي . أحجام الليفات العضلية في الأنثى صغير والتخطيط العرضي غير محدد ، أشرطة (Z) غير منتظمة وتكون غير موجودة أحيانًا . ضمور الليفات العضلية وعدم وضوح تخطيط القطعة اللحمية ، والميتوكوندريا قليلة جدًا والشبكة الساركوبلازمية موجودة بغزارة وتشر بوضوح إلى اتساعها . لابد من إجراء دراسات أخرى لمعرفة ما إذا كان ضمور عضلات الطيران في الأنثى البالغة يتطابق مع نمو المناسل أو أن العضلات لا تتطور في الطور البالغ .