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Comparative study of spiracular structure in some selected Blattidae (Dictyoptera)

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Abstract

The differences in structure and function of tracheal system of different species of cockroaches may give some clue to the differences in the action of different insecticides in gaseous and powder form. Hence the present study on the comparative structure of spiracles and their function was undertaken in *Blattella germanica* (L), *Periplaneta americana* (L), *Blatta orientalis* (Stoll) and *Supella longipalpa* (Serv.) belonging to family Blattidae of Order Dictyoptera. All the cockroach species studied possess 10 pairs of spiracles which is a full complement in the present day insects. The average spiracular aperture areas (mm^2) of 1st thoracic spiracle in the four cockroach species studied was 0.5, 0.28, 0.14 and 0.1 in *Periplaneta americana* (pa), *Blatta orientalis* (bo), *Supella longipalpa* (sl) and *Blattella germanica* (bg), respectively. The second thoracic spiracle measured 0.2, 0.08, 0.045 and 0.049 mm^2 in size in pa, bo, sl and bg, respectively. The first abdominal spiracle measured 0.08, 0.049, 0.03 and 0.019 mm^2 in size in pa, bo, sl and bg, respectively. Whereas average spiracular aperture areas (mm^2) of last abdominal spiracle was found to be 0.0295, 0.0275, 0.0053 and 0.0058 mm^2 in pa, bo, sl and bg, respectively.

In the present study both the lids of the 1st thoracic spiracle are equally developed in *Blattella germanica* (L), whereas the immovable lid gets reduced in *Periplaneta americana* (L), *Blatta orientalis* (Stoll) and *Supella longipalpa* (Serv.). Maximum reduction is observed in immovable lid of 1st thoracic spiracle of *Blatta orientalis* (Stoll).

In cockroach species studied, the external type of spiracular regulatory mechanism is noticed in the thoracic and internal in the abdominal ones. But the fan shaped muscle found in both the thoracic as well as abdominal spiracles, whereas parallel cylindrical muscle has been observed in the abdominal ones. The position of all the spiracles in other 3 Blattids is the same just as described in *P. americana* (L). The first and second thoracic spiracles show very little deviation from the basic plan as seen in *P. americana*. The structural differences are mainly conspicuous in the abdominal spiracles of different species.

Keywords: Insect respiration, spiracle, structure, blattidae, tracheae

Introduction

The animals developed special mechanical devices for respiration which is called respiratory system, the tracheal system in insects constitute the tracheal tubes which open at body surface through the openings, the spiracles.

Spiracles are lateral in position usually on the pleura of the thoracic and abdominal segments but their exact position is very variable. In most of the insects it is seen that in case of abdomen, the spiracles are located in between the soft tergal and sternal membrane, sometimes anteriorly or posteriorly of its segment.

The respiratory system may be classified on the basis of the number and distribution of the functional spiracles [12]. The system of spiracular classification applicable to larvae can hardly be used profitably for the adult of the same [10]. The criteria used for dipteran spiracular classification do not suit for those of Hymenoptera [19, 20].

Since cockroaches are important pests of households, granaries, godowns, eating houses etc. and they are widely distributed throughout the world, it is most necessary to control them. The most useful method of their control is by use of insecticide. The insecticides which can be used to control roaches may be either contact powder or liquids or they may be in the gaseous form. Since gaseous insecticides act via the tracheal system, it is important to study this system in cockroaches. The differences in structure and function of tracheal system of different species of cockroaches may give some clue to the differences in the action of different insecticides in gaseous and powder form. Hence the present study on the comparative structure of spiracles and their function was undertaken. It will not only enrich our knowledge on the action of insecticides but may add some knowledge on phylogenetic relationships of different species and genera in the order Dictyoptera.

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The simplest type of spiracles was found to occur in Apterygotes and Pterygotes like plecoptera, where the spiracular apertures are mere invaginations of the integument which further continue as tracheae. The opening of the latter is at the base of the spiracular atrium, sometime the outer opening. The peritremal ring may be guarded with lips or raised or produced into a pair of valve like plates.

The spiracular surrounding is often full of a variety of outgrowths such as spines, ridges, tegumentary folds, lamellae. All of these are cuticular which may resemble secondary projections. These processes may block the openings or protect the structure. The type of regulatory mechanisms such as external closing mechanism and internal closing mechanism has been described by many entomologists [16]. Burmeister [5] believed that the valves present as closing devices of spiracular apertures prevented the entry of dust particles and parasites.

As the spiracles and associated parts are integumental in origin, the development of external or internal closing mechanism would primarily depend upon the relative degree of sclerotization of chitinous integument surrounding the spiracle [19, 20, 21]. Weis-Fogh [23] has reported a rubber-like chito- protein called "resilin" which is known for its highly extensile and contractile properties.

Although muscles vary considerably in size and mode of action, they could be divided into two categories on the basis of their shape and arrangement: (a) Cylindrical or parallel shaped muscles in which the fibers are arranged in bundle or (b) fan shaped muscles in which fibre radiates from the point of attachment [16]. The latter type (b) of muscles is found in roaches.

Many attempts have been made to classify spiracles based on various characters. A general classification applicable to all the spiracles was proposed by Tonapi [19, 20] based on the type of closing apparatus. He concluded that the external type included the movement of lids, a pronotal occlusor sclerite and an operculum or membranous flaps; and the internal type possessed either callipers, lever actuated flap valves or lever compression of the atriotracheolar junction. He also presented an alternate classification based on the shapes of the muscles - an acicular occlusor of the first thoracic spiracles or parallel fibers in cylindrical muscles found in the abdominal spiracles.

The frequency of ventilation of intact resting cockroaches was studied with Kymographic techniques [4]. The respiratory systems of some Blattids have been earlier studied by Telang [18] which focus mainly on morphology, physiology and some mechanisms evolved in the system. Active ventilation of the respiratory system is a common behavior observed in most large or highly active insects, including locusts, cockroaches, beetles and honey bees [6, 7 & 8], as well as lepidopteran and dipteran pupae [13 & 22]. The respiratory system of the hissing cockroach, *Gromphadorhina portentosa*, functions as a unidirectional pump through the coordinated action of the spiracles and abdominal musculature [11]. The differences in location, structure and function of spiracles of different species of cockroaches may give some clue to the differences in the action of different insecticides in gaseous and powder form. It will add some basic information on morphological features of spiracles. It will not only enrich our knowledge on the action of insecticides but may add some knowledge on phylogenetic relationships of different species and genera in the insect orders. Hence the present study on the comparative structure of spiracles and their function was undertaken.

Materials and methods

Identification and Collection of the Species

The four species which are used for present studies are described below

The American cockroach (*Periplaneta americana*-L)

It is a common cockroach found in canteens, kitchens, latrines, dark marshy places. They are reddish brown except for a light brown margin around the side and back edges of the pronotum. They are large insects with both male and female being winged, about 1^{1/2} inches in length and bearing long active antennae. They hide under crevices during day time and seen moving during night time.

The German cockroach (*Blattella germanica* - L)

This cockroach is also found mainly in canteens, kitchen rooms, marshy places etc. It is pale brown with 2 parallel dark stripes on the pronotum. When full grown it is 1/2 to 5/8 inch long, boat shaped in appearance and possesses full developed wings covering the abdomen. It has antennae longer than the body. Wings are functional but only for downward flight. It is the most active among all the species.

The oriental cockroach (*Blatta orientalis* or *Stylopyga orientalis* – Stoll)

Found in homes and other buildings where dark protected areas, food and water are available. They are shiny black, occasionally wings of male are mahogany coloured. Female is oval and has only wing stubs. Length of female is about 1^{1/4} inch. Males have developed wings partially covering the abdomen. They are more slender about 1 inch long. This species is provided with whitish or yellowish stripes on both sides of thorax and abdomen.

Brown banded cockroach (*Supella longipalpa* – Serv.)

Dimorphic cockroach is about the size of the small German cockroach but bears a light tan band across the center of the wings. Male has functional wing covering the tip of its slender abdomen and female is broad with stubby wings. It is found in soil near marshy places, debris and poultry food sheds. The adult roaches were collected from various localities such as brown banded cockroach and oriental cockroach from Jalgaon and. American cockroach and German cockroach from Ahmednagar College campus. These were used freshly or were preserved in 5% formalin and can be reared [14].

In studying the spiracular structures in different cockroaches the practice of using abbreviations has been followed. These acronyms are already accepted in the recent literatures [9] which are as follows:

- (i) *Periplaneta americana* (L) - P. a.
- (ii) *Blattella germanica* (L) – B. g.
- (iii) *Blatta orientalis* (Stoll) – B. o.
- (iv) *Supella longipalpa* (Serv) – S.l.

Collection of the Spiracles: Technique

The spiracular openings are small brownish areas located in the soft membranes. The first and second thoracic spiracle are between the first and second and between second and third pair of legs respectively. The first abdominal spiracles are on dorsolateral side of first abdominal segment and are most prominent. Other abdominal spiracles are between the terga and sterna of the abdominal segments.

Thoracic Spiracles

Spiracles are situated on a very small, slightly brownish area in between the dorsal portions of the legs. These were removed by holding the cockroach and stretching either the first and second legs or the second and third legs respectively for first or second spiracles. By cutting the membrane all around, the spiracle the latter were collected in the cavity blocks.

First Abdominal Spiracles

After cutting the wings at the bases, these spiracles were removed with scissors or arrowhead by cutting the area around dorsolateral sides of the 1st abdominal segment.

Abdominal Spiracles

By cutting the lateral side of the abdomen and the laterally cut portion of the abdomen were placed on a slide with 2 drops of water. The cut piece of the abdomen was kept in such a manner that the terga and the sterna are stretched. Fat bodies, tracheae and other excessive materials such as terga and sterna cleared off. Each spiracle was separated with fine needles and was kept in separate cavity block. Freshly narcotized (with chloroform or ether) roaches were observed under binocular microscope to study the visible external movable parts. And it was easy to separate the spiracular structure in fresh specimens than preserved ones, because in preserved specimens the elasticity of the parts was lost. For detailed anatomical studies the sclerites and other membranous structures surrounding the area were removed as described above and fixed in Bouin's fluid. The spiracles were stained with 0.5% eosin in 95% alcohol, which gives best results. Mallory's Triple stain could also be used but it was very difficult to locate the material in solution C which is black in colour. Sometimes it stains dark and this method is also time consuming. In some instances where spiracles do not stain it was found necessary to bleach the cuticle with chlorine vapours or hydrogen peroxide prior to staining. The cuticular parts were observed by dissolving muscles etc. in boiling 10% KOH. The stained spiracles were dehydrated and then cleared in clove oil. After this, it was necessary to treat the material in xylene which removes the oil. Spiracles were then mounted in DPX. Before putting cover slip excess cuticular parts were removed. The material was then oriented

on the slide in such a manner that either internal view or external view of the spiracle was observed, Cover slip was placed gently with the help of a needle.

Slides were kept at 40 °C temperature in oven till they dried. Thus stained mounts of the dissected spiracles and their associated parts were prepared for further observations on the cuticular outgrowths and designs. Special attention was given to the differences, if any, in their size and architecture in different species. The illustrations were made to scale using ocular micrometer and compound microscope. Only one microscope and magnification was used throughout the study.

Results

Spiracular Structures

An account of the morphology of the thoracic and abdominal spiracles of *Periplaneta americana* (L) is given in detail and those of the other species has been dealt by comparison. There are ten pairs of spiracles of which two are situated in the thorax and the remaining eight lie in the abdomen (Holopneustic type). The thoracic spiracles are located in the intersegmental pleural membranes just above the bases of the legs in their respective segments, while the abdominal ones assume a lateral position. The average areas (mm²) of all the spiracular apertures not only vary in different species, but also the average area (mm²) of different spiracles differ in the same species (Table 1 and Fig. 1)

The thoracic spiracles possess an external closing mechanism. They are with lids, muscles and sclerotic process for muscle attachment. The abdominal spiracles differ from the thoracic ones in closing mechanism and the other structures useful for the internal closing mechanism. In this type the occlusor apparatus lies at the inner end of the atrium regulating the size of the tracheal orifice. The walls of the atrium and secondary atrium of the spiracles of all the species studied have a tessellated (like a hanging bunch of cords) appearance. The cells are shaped as squares, pentagons hexagons or octagons and are approximately 0.01 mm in size [18]. There are five to six cells grouped around the base of setae in the atrium. The setae are also found on the peritremal sclerite of the 1st and 2nd thoracic spiracles of all species.

Table 1: The average spiracular aperture areas (mm²) of the ten spiracles in the four cockroach species.

Spiracles	<i>P. americana</i> (L) mm ²	<i>B. orientalis</i> (Stoll) mm ²	<i>S. longipalpa</i> (Sarv) mm ²	<i>B. germanica</i> (L) mm ²
I Thoracic	0.541	0.2800	0.1446	0.1195
II Thoracic	0.2340	0.0864	0.0450	0.0498
III(Ist Abdominal)	0.0843	0.0496	0.0316	0.01920
IV	0.0235	0.0129	0.0034	0.0026
V	0.0287	0.0156	0.0032	0.0026
VI	0.0280	0.0121	0.0024	0.0027
VII	0.0227	0.0180	0.0032	0.0024
VIII	0.0175	0.0125	0.0028	0.0030
IX	0.0173	0.0133	0.0033	0.0031
X (last Abdominal)	0.0295	0.0275	0.0053	0.0058

The average spiracular aperture areas (mm²) of 1st thoracic spiracle in the four cockroach species was 0.5, 0.28, 0.14 and 0.1 in *Periplaneta americana* (pa), *Blatta orientalis* (bo), *Supella longipalpa* (sl) and *Blattella germanica* (bg), respectively. The second thoracic spiracle measured 0.2, 0.08, 0.045 and 0.049 mm² in size in pa, bo, sl and bg,

respectively. The first abdominal spiracle measured 0.08, 0.049, 0.03 and 0.019 mm² in size in pa, bo, sl and bg, respectively. Whereas average spiracular aperture areas (mm²) of last abdominal spiracle was found to be 0.0295, 0.0275, 0.0053 and 0.0058 mm² in size in pa, bo, sl and bg, respectively.

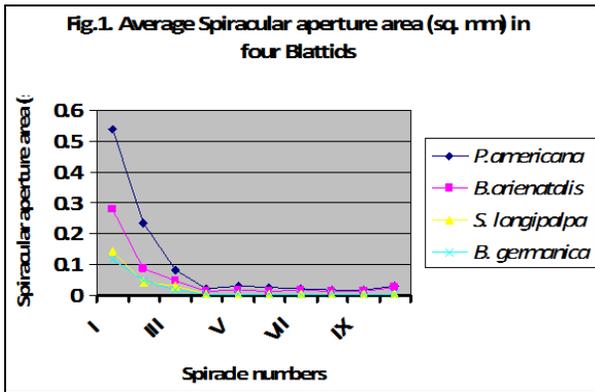


Fig 1: The average spiracular apertures areas (mm²) of the ten spiracles in the four cockroach species: (A) *P. americana*; (B) *B. orientalis*; (C) *S. longipalpa*; (D) *B. germanica*.

Periplaneta americana

First Thoracic Spiracle (Fig. No. 2 a)

The first thoracic spiracle is the largest of all spiracles studied. It is situated ventrally in the intersegmental pleural membrane between the pro and mesothorax. The spiracle is lodged in a small sclerotic plate known as the peritremal sclerite. The peripheral edge of the latter is slightly thickened. The external opening known as the atrial or spiracular opening is an elongated fissure situated

transversely in the peritremal sclerite. The opening is guarded by a pair of bilobed valves or lids. Both lids are elevated extensions of the peritremal sclerite.

The anterior lid is large and movable like a flap while the posterior one is small, rigid and stationary. The spiracular orifice leads into a shallow atrial chamber which is formed by the inner surface of the two lids and opens into trifold trachea. A chitinous process arises from the center of the movable lid and projects towards base of the atrium. The distal end of this process is curved for the attachment of muscle. An ocluser muscle which originates from the peritreme is inserted on the free curved end of chitinous process. At the base of the atrium, the three tracheal openings are separated from each other by two septa. The septum which separates the anterior two tracheae is thickened and particularly the free end projecting towards the movable lid becomes broad. The dilator muscle takes origin below the ocluser from the peritreme and is inserted on the broad end of the septum. By the contraction of the ocluser muscle the movable lid approaches towards the stationary one thereby closing the fissure between them. When the ocluser muscle relaxes and the dilator contract, a pull is exerted on the septum and the movable lid is drawn away from the fissure affecting the opening of the spiracular orifice.

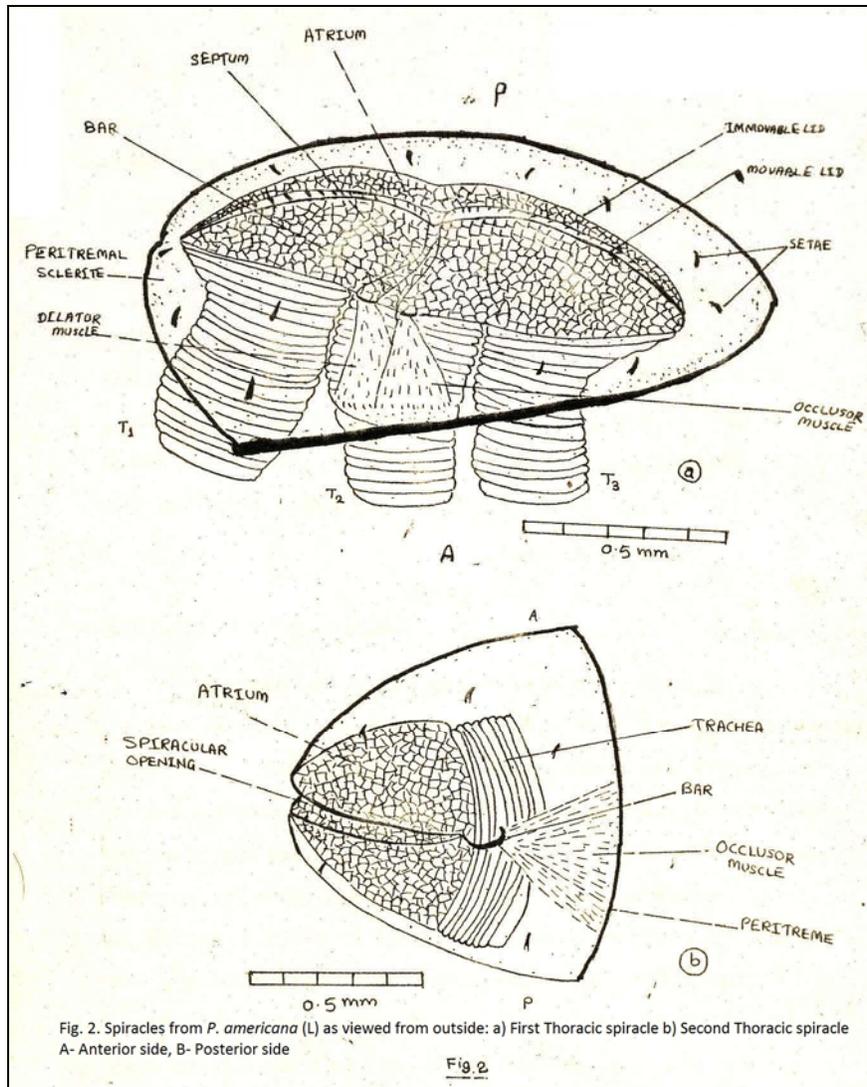


Fig. 2. Spiracles from *P. americana* (L) as viewed from outside: a) First Thoracic spiracle b) Second Thoracic spiracle A- Anterior side, B- Posterior side

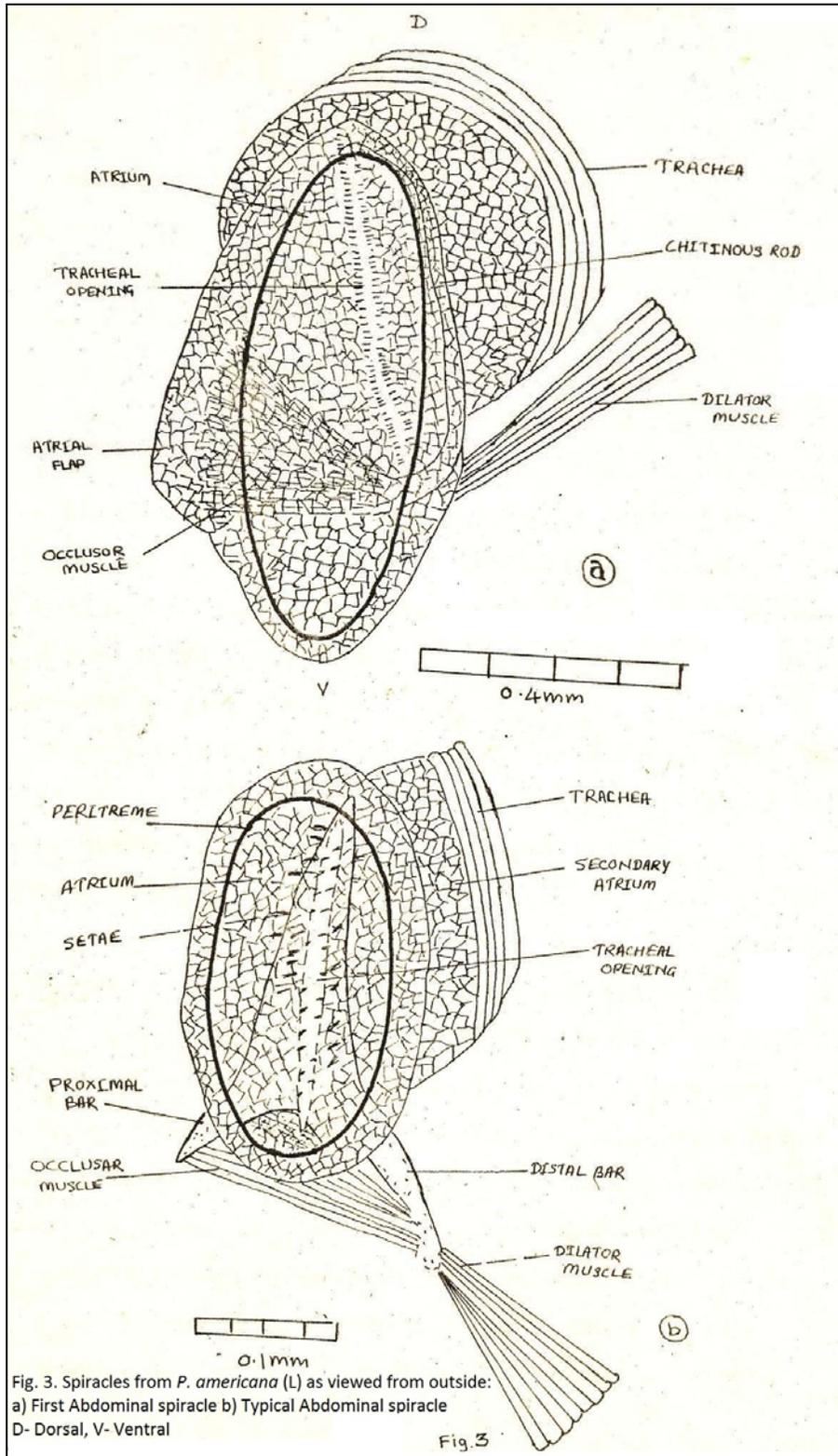
Fig. 2

Second Thoracic Spiracle (Fig. 2 b)

The second thoracic spiracle is lodged in the intersegmental membrane between the meso and metathoracic pleurons. Both the lids are movable and are strengthened by a thin chitinous rim. The latter borders the semicircular atrial orifice. The setae are found to border the posterior or upper lid only. Below the opening is an atrial chamber formed by the inner surface of the lids. The atrium at the inner end opens into a trachea. A small chitinous curved process is given out on the inner side at the base of the two lids. An

occludor muscle originates from the peritreme and is attached to the sclerotic process. When the muscle contracts, the chitinous process is pulled and the lids are brought together along the midline thereby closing the outer semi-circular spiracular opening. On the relaxation of the occludor muscle the valves return to their normal position by the elasticity of their two basal hinges.

First Abdominal Spiracle (Fig. 3 a)



The first pair of abdominal spiracles shows the variation in its position and morphology. It is largest of all abdominal spiracles, situated on the antero-lateral margin of the first abdominal tergum, orifice is elongated slipper shaped leading in to sclerotized atrial chamber which opens in to secondary atrium from where trachea initiates. This tracheal opening is a narrow slit situated obliquely guarded by regulatory apparatus situated between the atrium and the secondary atrium. Distally a chitinous curved rod arises from the anterior end of the tracheal opening and on the proximal side of the spiracle the atrial wall gives out a flap like process. A fan shaped ocluser muscle originates from the flap like projection and is inserted on the free end of chitinous rod. A dilator muscle originates from the tergum. The fibers of dilator muscle are arranged in parallel bundles. The contraction of the ocluser muscle presses the lever against the tracheal opening thereby closing the orifice; the relaxation of it simultaneously leads to contraction of dilator muscle that opens the tracheal orifice.

Typical Abdominal Spiracle: (Spiracles 4-10) (Fig. 3 b)

All the remaining abdominal spiracles are more or less of the same size except the last one which is larger than the others. The abdominal spiracles are situated on the downwardly deflected lateral position of the tergum with their longitudinal axis lying vertically. They are located such that their apertures face the posterior end of the body. The spiracular opening is oval in shape bordered by thin sclerotic peritremal ring. It leads into a hollow atrium, at the base of which is situated a vertical slit of the tracheal opening. Very

few chitinous outgrowths project into the lumen of the tracheal orifice. Nevertheless, setae are found scattered in the atrial cavity around the tracheal opening. The atrial cavity leads into the secondary atrium which further opens into the trachea. The regulatory apparatus is situated at the juncture of the atrium and secondary atrium. This apparatus operates by a simple pinch-cock mechanism.

A pair of levers or bars is situated on either sides of the orifice in the form of proximal and distal apodemes, between the distal ends of which an ocluser muscle is stretched. The dilator muscle originates from the tergum and is inserted on the free end of the distal apodeme. The contraction and relaxation of the ocluser muscle brings the two bars together and pulled away the distal from the proximal one, thereby closing and opening of the tracheal aperture, respectively.

The basic principle involved in the regulatory mechanism and the position of all the spiracles is same for the four cockroach species studied. The first and second thoracic spiracles showed very little deviation from the basic plan as seen in *P. americana* (L). The abdominal spiracles showed conspicuous structural differences.

***Supella longipalpa* (Serv.)**

First and Second Thoracic Spiracles (Fig. 4a & 4b)

Both the thoracic spiracles of the species show close resemblance to those of *P. americana*. The outer opening of the first thoracic spiracle is situated towards the anterior border of the peritremal sclerite. The movable and the immovable lids enclose a well-developed atrial cavity.

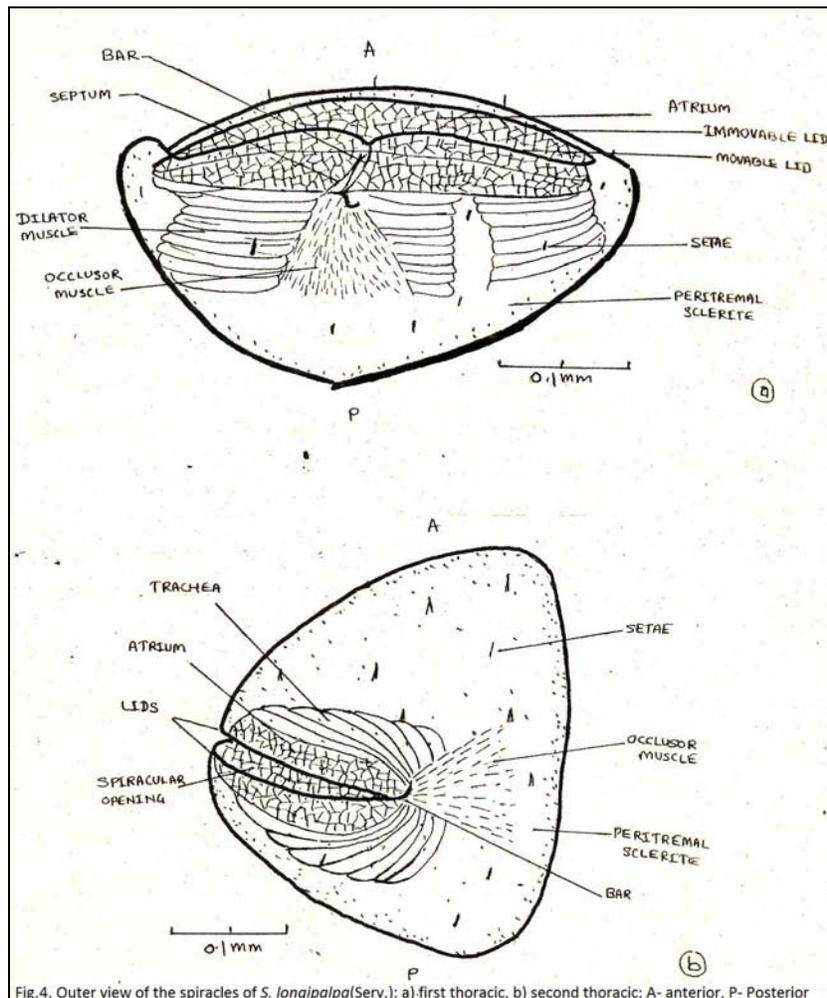


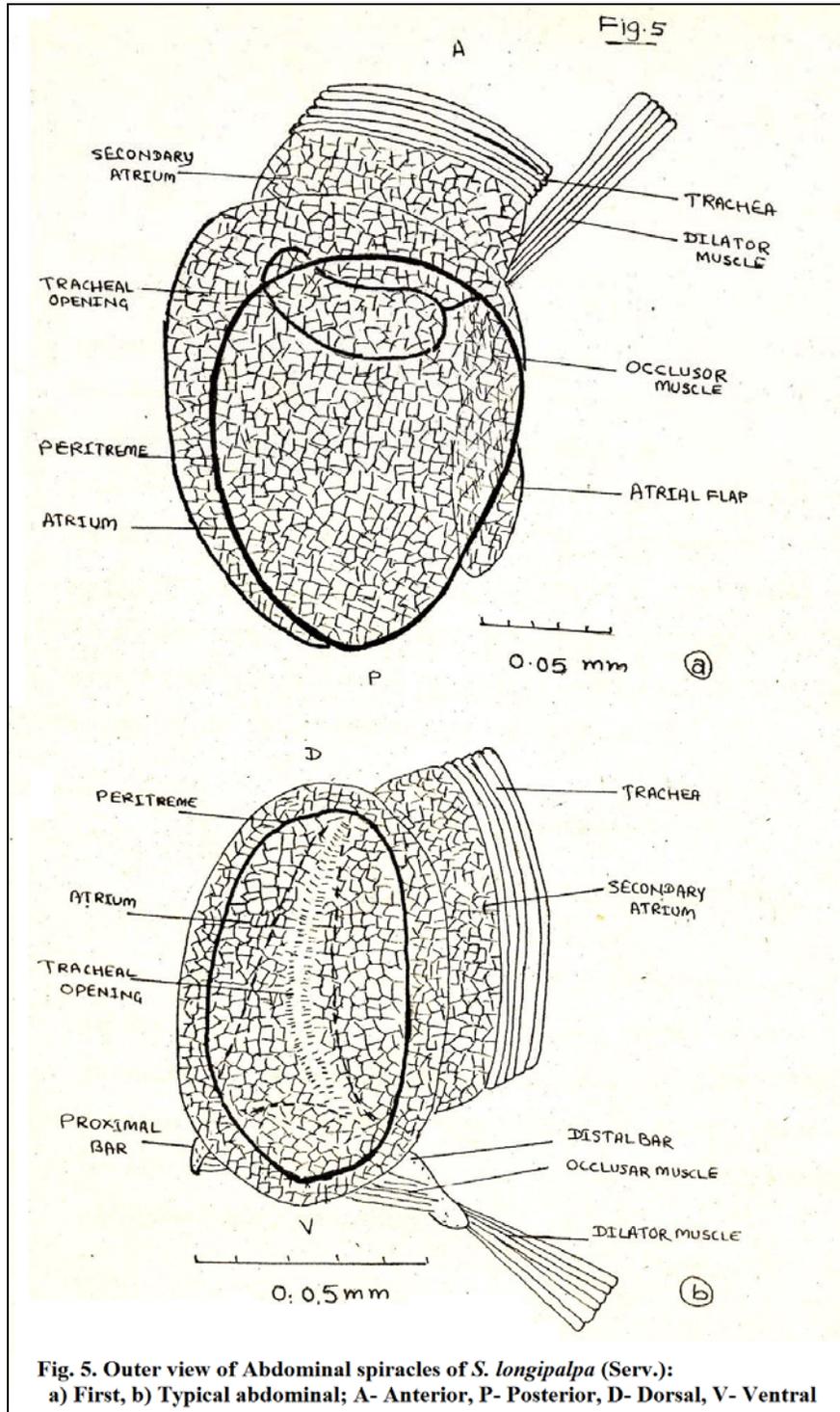
Fig.4. Outer view of the spiracles of *S. longipalpa*(Serv.): a) first thoracic, b) second thoracic; A- anterior, P- Posterior

First Abdominal Spiracle (Fig. 5 a)

The external opening of the first abdominal spiracle is oval with the anterior part relatively broad. The atrial cavity is shallow wide and oval in shape. A transverse semi-lunar tracheal opening is situated anteriorly at the base of the atrium. The tracheal opening is without setae and is bordered by a thin sclerotic rim. The atrium gives rise to a flap like projection on the distal side of the spiracle. Moreover, a small transverse curved bar originating at the tracheal opening is also situated towards the distal side of the spiracle. Since in *S. longipalpa* (Serv.) the free end of the rod and the flap are situated on the distal side the occlusor

muscle extends below the distal border of the spiracle. On the outer side of the rod is inserted a dilator muscle which originates from the tergum. The dilator muscle has cylindrical appearance. The contraction of the closing muscle presses the lever against the tracheal opening and thus the tracheal orifice is closed. When the occlusor muscle releases, the simultaneous contraction of dilator muscle opens the tracheal opening which leads into a secondary atrium which further opens into the trachea.

Typical Abdominal Spiracle (Fig. 5b)



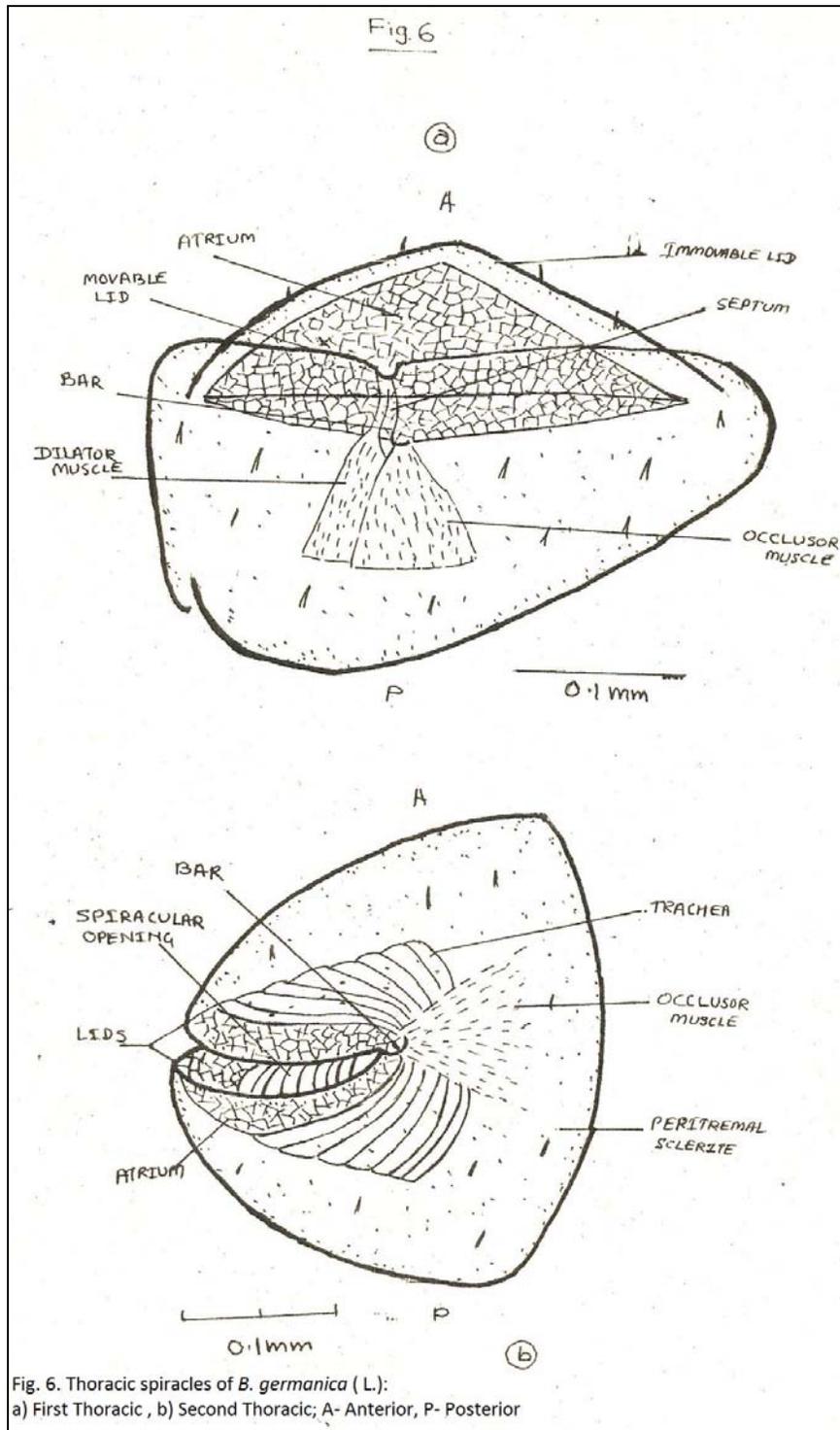
The outer opening of a typical abdominal spiracle is oblong and opens into a hollow atrial cavity. At the base of the atrium is a vertical crescentic opening. This opening is bordered by setae projecting into the lumen. The tracheal aperture is strengthened by a proximal triangular and an elongated curved distal bar which is longer than the proximal triangular bar. An occlusor muscle is stretched between the inner sides of the distal ends of the two bars. While the dilator muscle originates from the deflected portion of the tergum and is inserted on the free end of the distal bar opposite the attachment of the occlusor muscle. The contraction of the occlusor or closing muscle brings the two bars together, thereby constricting the tracheal orifice. With

the relaxation of the occlusor and subsequent contraction of the dilator muscle, the distal bar is pulled away from the proximal one to facilitate the opening of the tracheal aperture. The secondary atrium which leads into trachea is present.

Blattella germanica (L)

First and Second Thoracic Spiracles (Figs 6a & 6b)

The outer opening of the first thoracic spiracle is situated at the anterior most end of peritremal sclerite. The stationary lid is well developed, but the movable one is reduced. The second thoracic spiracle resembles that of *P. americana* in both morphology and regulatory mechanism.



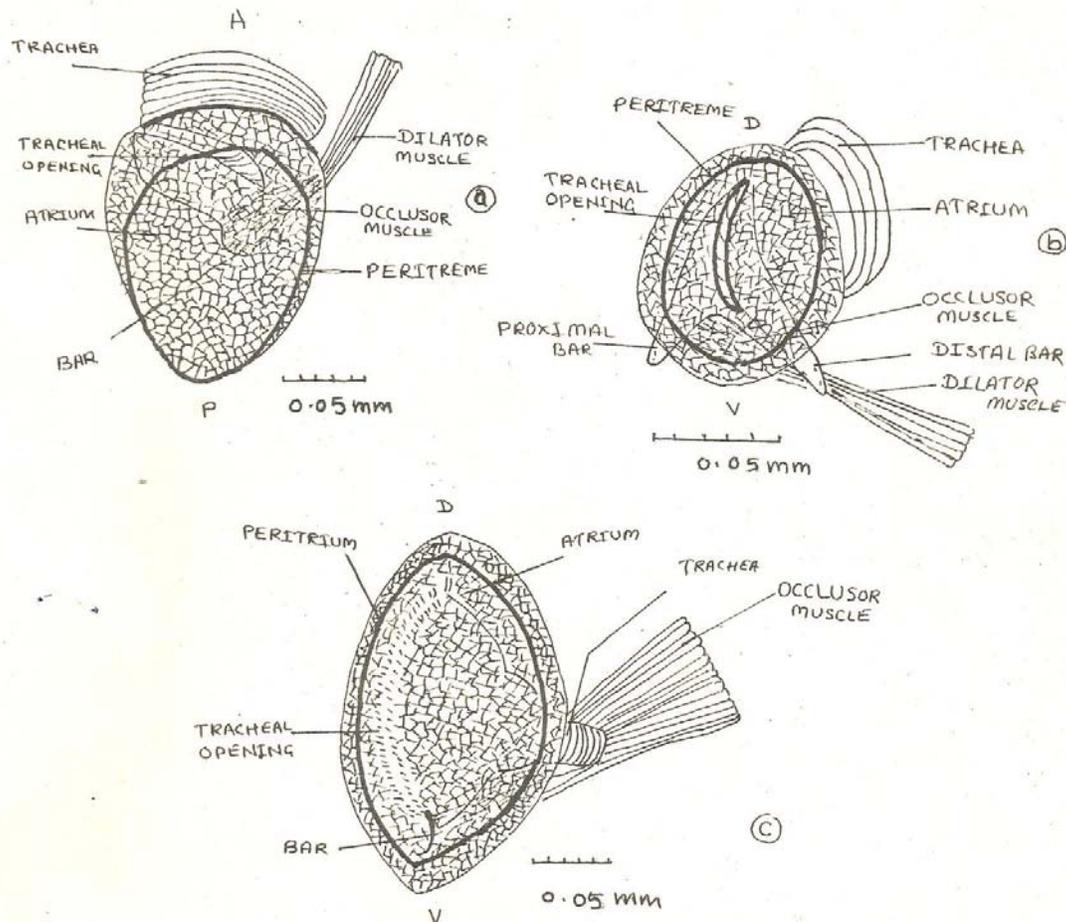
First Abdominal Spiracle (Fig. 7 a)

Fig.7. The Abdominal spiracles of *B. germanica* (L.) as seen from outside: a) First, b) Typical, c) Last abdominal
A- Anterior, P- Posterior, D- Dorsal, V- Ventral

The outer opening of the first abdominal spiracle is oval. The tracheal orifice is an oblique opening situated anteriorly in the atrium and is devoid of only sclerotized projections. The tracheal aperture is surrounded by a thin sclerotic rim. Two curved bars arise from the proximal end of the tracheal opening which runs distally on either sides of the orifice. The occlusor muscle is stretched between these two bars. Thus, the first abdominal spiracle in this species does not give rise to atrial projection for the muscle attachment. The secondary atrium is absent and the atrium opens into the trachea.

Typical Abdominal Spiracle (Fig. 7 b)

The outer opening is oval and leads into a spacious and hollow atrial cavity. The tracheal aperture is a vertical elongated crescentic slit in the atrium and is without setae. Pair of broad sclerotic bars is situated on either sides of the tracheal opening. The proximal bar is short and thicker, while the distal one is longer. The atrium directly leads into trachea.

Last Abdominal Spiracle (Fig. 7 c)

The last abdominal spiracle differs considerably in size, morphology and regulatory mechanisms from the typical abdominal spiracle and hence is described here independently. The spiracular opening is D, shaped and

opens into a shallow atrial cavity. The tracheal aperture is vertical elongated crescentic opening situated towards the proximal side of the atrial cavity. From the lower end of the tracheal orifice arises a small curved rod. A large fan shaped muscle arises from the deflected margin of the tergum and is inserted on the curved rod. The contraction of this muscle opens the tracheal orifice while relaxation brings about the closure. There is no dilator muscle. There are numerous setae projecting into the centre of the tracheal opening. The atrium leads into a special cup like region with taenidia which tapers and continues, after suffering a constriction, further as a true tracheal tube.

Stylopyga* or *Blatta orientalis* (Stoll.)*First Thoracic Spiracle (Fig. 8a)**

It is smaller than the *P. Americana* & is situated in a more oblong peritremal sclerotic plate. The spiracular opening is a transverse slit guarded by a pair of unequal lids. The movable lid is relatively better developed while the rigid one is considerably reduced thin. Both the lids are provided with setae on marginal sides. The atrium formed by inner wall of the immovable lid is also reduced. In this species the maximum reduction of the immovable lid is observed. In all other respects the spiracles are essentially similar to the corresponding spiracles in *P. americana*.

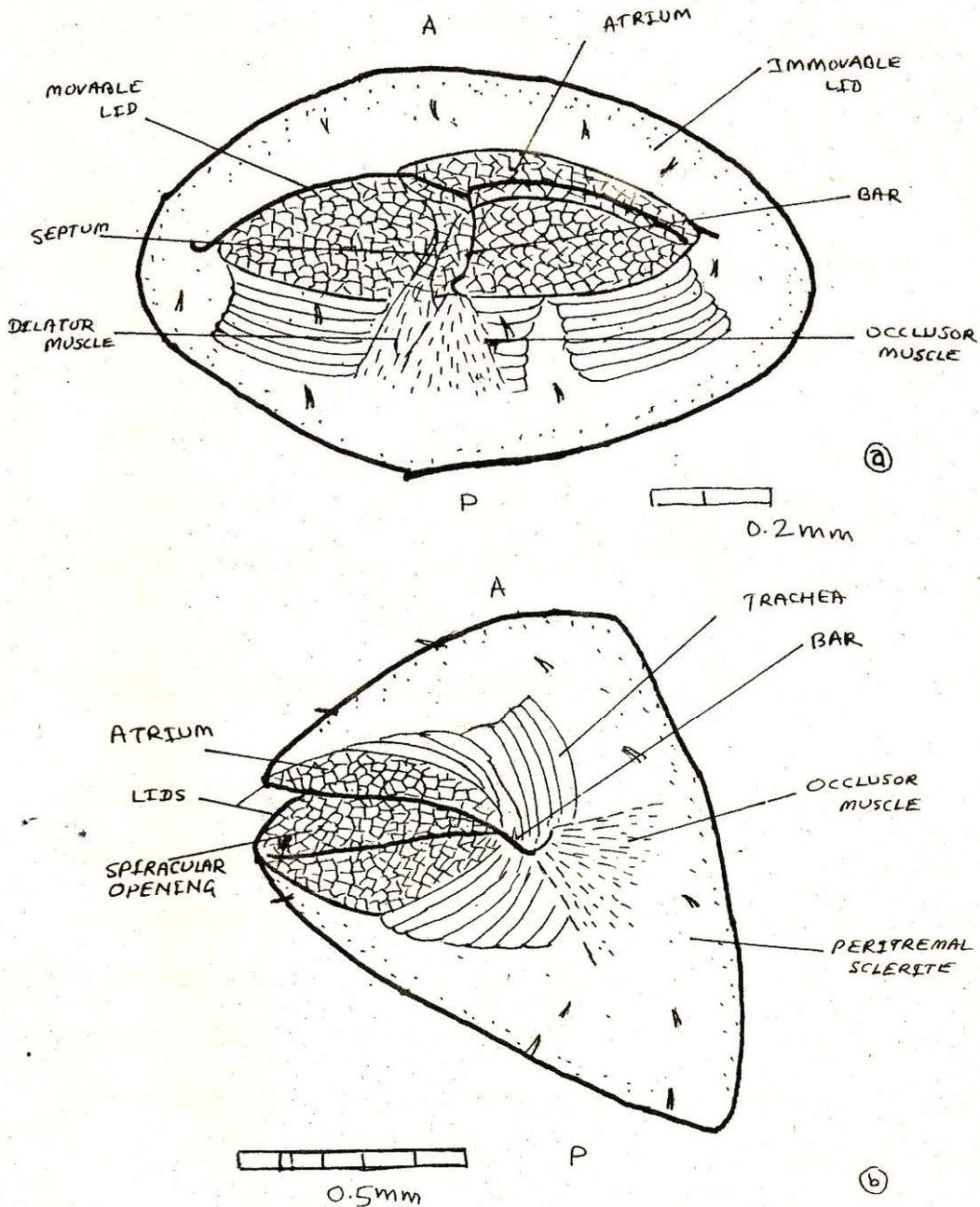


Fig.8. *B. orientalis* (Stoll.), Spiracles-external view a) FirstThoracic spiracles, b) Second Thoracic spiracles
A- anterior, P- Posterior

Fig. 8

Second Thoracic Spiracle (Fig. 8 b)

It doesn't show any difference in the basic structure. Both the lids are well developed. The peritremal ring surrounding the upper lid is thin while that of the lower lid is thicker. The atrium formed by the inner wall of the lower lid is larger than the one on the side of the upper lid.

First Abdominal Spiracle (Fig. 9 a)

The opening of the first abdominal spiracle is oval and surrounded by a thin sclerotic peritremal ring. The atrial

cavity gives out a well-developed flap like projection for the attachment of the occlusor muscle. The tracheal opening is a long oblique slit situated in the atrial base. The tracheal orifice is surrounded by numerous rigid spiny setae which are directed towards the lumen of the opening. The distal side of the tracheal opening is strengthened by a long chitinous bar which serves for the attachment of the dilator as well as for the occlusor muscle. The atrium opens into a secondary atrium which leads to the trachea.

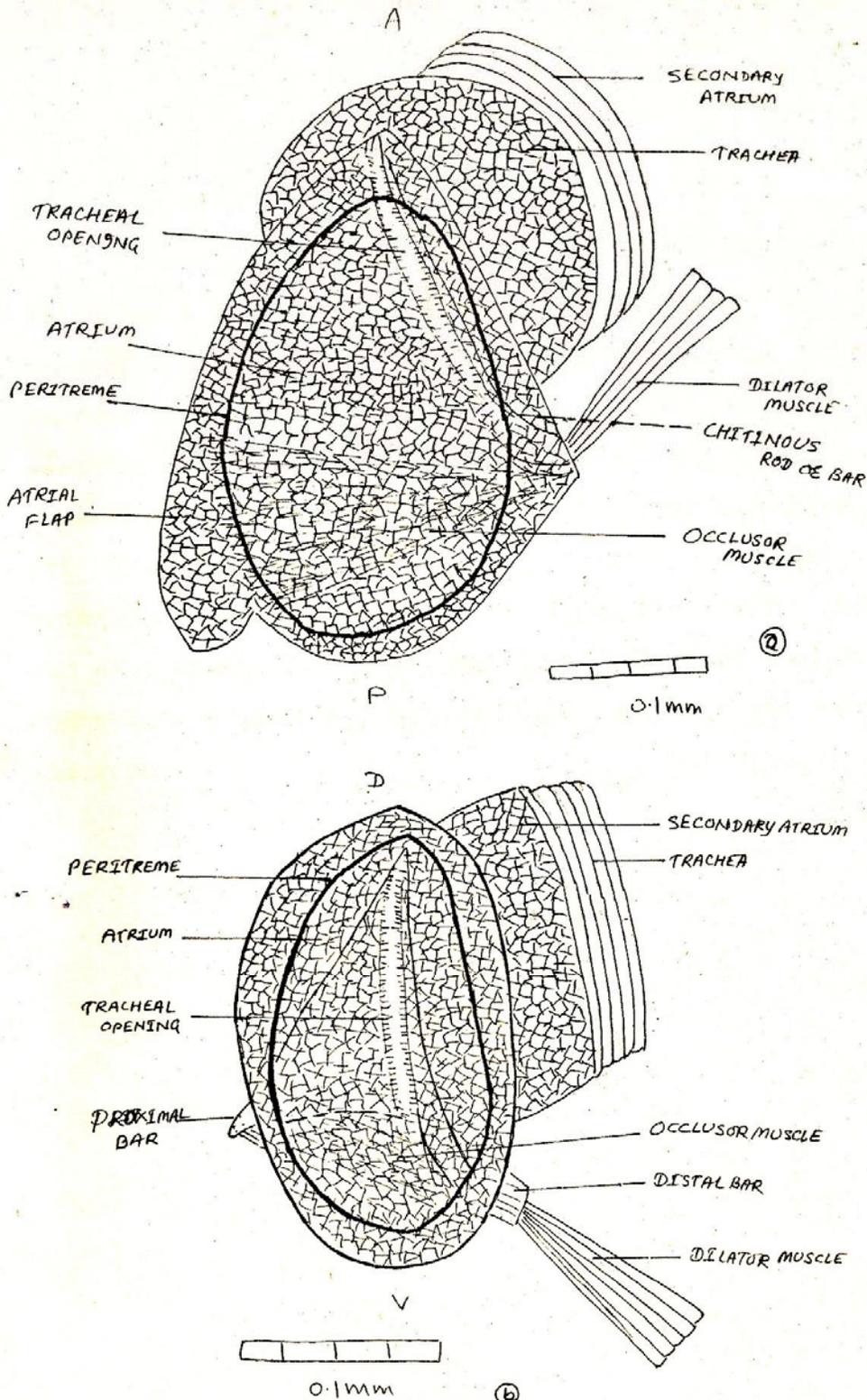


Fig.9. The abdominal spiracles of *B. orientalis* (Stoll.): External view; a) First abdominal, b) Typical abdominal
 A- Anterior, P- Posterior, D- Dorsal, V- Ventral
 Fig. 9

Typical Abdominal Spiracle (Fig. 9 b)

The spiracular aperture of the typical abdominal spiracle is an oblong opening which leads into a well-developed atrium. The tracheal opening is an elongated fissure situated at the base of the atrial cavity, parallel to the outer opening. Chitinous projections present in the tracheal orifice are

strengthened by a pair of unequal bars. The proximal bar is large and triangular while the distal one is comparatively slender and elongated. In all the abdominal spiracles the atrium opens into a secondary atrium which further leads into the trachea.

Discussion

Comparative studies have been made on the spiracles of Orthoptera [1, 16, 17]; Diptera, Thysanura, Mecoptera and Trichoptera [10]; Hymenoptera [19, 20] and Hemiptera [2]. The prime purpose of all such studies has been to use spiracular number and characters to indicate the genetic affinities, evolutionary and phylogenetic relationships of various insects' orders. There seems to be no general rule applicable to the number of spiracles in different orders of insects. Even within a single order, the numbers of spiracles are reduced in many families [15, 19 & 20]. The presence or absence of a particular pair of spiracles and reduction in the number of spiracles from the typical classical number of 10 pairs in any stage of insect development constitutes an evolved condition may be disputable. In any case, since the primitive number of spiracles as well as many other insect species have larger number of spiracles, it is safe to assume that the reduction in their number has been as a consequence of acquisition of abilities to do away with larger number of spiracles. While on one hand, the increased number of spiracles may be welcome to supply more oxygen to the tissues, it is equally dangerous to expose the internal tissue fluids to unnecessary and uncontrollable levels of desiccation. Perhaps, therefore, the rational maximum number of 10 pairs of spiracles in any adult insect must have been a crucial step in the evolution of the tracheal system. All the cockroach species studied possess 10 pairs of spiracles which is a full complement in the present day insects, has been found in all cockroach species expected, since Dictyoptera constitute an ancient group formed early in the evolution of insects.

In the first thoracic spiracles of Blattids approximately one third of the total tracheal openings are separated by a thick septum. This arrangement, in which a large cephalic tracheal trunk takes its origin from the conspicuous openings in the spiracle formed by the thick septum, is significant. It is a remarkable adaptation exhibited by these insects to separate the cephalic and thoracic respiratory pathways. This unique feature of the first thoracic spiracle is perhaps to promote an efficient aeration of the central nervous system which has to remain hypersensitive to the small environmental changes. The considerably larger size of the 1st thoracic, 2nd thoracic and the first abdominal spiracle is a probably due to the major role of aerating the cephalic and thoracic regions which are centres of intense physiological activities. A comparatively large size of the last abdominal spiracle is perhaps to enhance the efficiency in tracheation of the reproductive organs. Such difference between the thoracic and abdominal spiracles has been commonly reported in respect of their size, shape, structure and closing mechanism [2, 19, 20].

The spiracular morphology and closing mechanism not only differ in different groups of insect order, but also show remarkable variations in the ontogeny even in the same species. The fine cuticular elements show differences even in the spiracles of the same insect. This situation is further complicated by the fact that the elastic regulatory devices occupy variable position in different spiracles of the same insect. It has therefore, not been possible to use such micro characters in the classification, systematics or taxonomic and phylogenetic studies. The regulatory approach of the spiracle plays a vital role in both the gaseous exchange and diffusion of water vapour. In Orthoptera, Dictyoptera and related groups the comparatively larger thoracic spiracle are inspiratory and hence a large amount of water loss through these spiracles is unlikely to occur.

Moreover, as inhalation is a slower and less active process, it can occur easily and quickly through the large thoracic spiracle. Snodgrass thought that the external type was restricted to thoracic and internal one to the abdominal spiracle.

Hassan [10] believed the external type which including movements of the lids or membranous flaps is a primitive condition. The presence of one rigid and one movable lid is the most primitive condition [12]. In the hissing cockroach, *Gromphadorhina portentosa* spiracles on different abdominal segments were also highly coordinated with one another [11].

In the present study both the lids of the 1st thoracic spiracle are equally developed in *Blattella germanica* (L), whereas the immovable lid gets reduced in *Periplaneta americana* (L), *Blatta orientalis* (Stoll) and *Supella longipalpa* (Serv.). Maximum reduction is in *Blatta orientalis* (Stoll).

In cockroach species studied, the external type of spiracular regulatory mechanism was noticed in the thoracic and internal in the abdominal ones. But the fan shaped muscle found in both the thoracic as well as abdominal spiracles, whereas parallel cylindrical muscle has been observed in the abdominal ones. External type is primitive condition as the thoracic spiracle has undergone lesser modifications. The muscle played a major role both in evolution of the spiracles and formation of levers and bars. The external type of regulatory mechanism is coupled with fan shaped muscle and poorly developed levers for their attachments.

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