Comparative morphology of Vosseler's gland in two species of Oedaleus (Orthoptera, Acridae, Oedipodinae)

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ABSTRACT

The morphology of the thoracic repugnatorial gland and its associated musculature in adults and nymphs of *Oedaleus senegalensis* (KRAUSS) and *Oedaleus nigeriensis* UVAROV is described and compared.

A remarkable feature of the nymphs of *Oedaleus senegalensis* and related species is the emission, when disturbed, of a strongly aromatic fluid of supposedly repugnatorial function. At present the chemical composition of the fluid is unknown but the thoracic gland which secretes it has been described in *Oedaleus decorus* (GERMAR) (under the name *O. nigrofasciatus*) (DEGEER) by VOSSELER (1902). VOSSELER demonstrated the secretory nature of the glandular epithelium by histology and illustrated the cellular structure and gross morphology of the gland. He indicated that a similar gland existed in *O. senegalensis*. HOLLANDE (1926) gave a conflicting account of the gland in *O. decorus* which he mistakenly believed to consist simply of folds of glandular membrane behind the pronotum, which were supposed to be eversible like the glandular sac of *Acrotylus* (JANONNE 1938) which also secretes aromatic substances but without noticeable production of fluid.

This paper describes and compares the gross morphology of the gland and its associated musculature in *Oedaleus senegalensis* and *O. nigeriensis*.

MORPHOLOGY

Dissection of numerous nymphs and adults of O. *senegalensis* from Niger Republic, West Africa, preserved in alcohol or acetic alcohol, and freshly killed specimens, has established that the gland is present in all developmental stages, though relatively small in the first instar. The gland consists of a large, sligthly bilobate, thin-walled sac with glandular epithelium situated just beneath the dorsal surface of the pronotum. At its maximum development it may reach as far anteriorly as the intersegmental membrane between the pronotum and the mesonotum. The orifice of the gland is a transverse slit in the mid-line of the intersegmental membrane between the pronotum and mesonotum, only visible when the pronotum is pushed forwards (Fig. 1). The cuticular lining of the gland is continuous with the dorsal intersegmental membrane.

The gland and its associated structures in *Oedaleus senegalensis* are shown diagrammatically in dorsal view in Fig. 2. The gland is supplied with two special muscles not found in the related species *Locusta migratoria migratorioides* (R. & F.) (ALBRECHT 1953). These are a short retractor (RM) and a longer dilator (DM) muscle, both composed of several separate strands joined by membrane which lie close together when the gland reservoir is empty, but fan out when it is swollen with secretion. Both muscles arise from the anterior margin of the pronotum at its junction with the intersegmental membrane. They are closely associated with each other and the dilator is closely connected to the surface of the gland throughout its length, finally inserting on the ventral wall of the orifice. Contraction of the dilator muscle opens the gland orifice which is normally kept closed by the stiffness of its cuticular lining, and may also compress the reservoir itselfs, helping to expel the secretion. The retractor muscle is inserted on the outer edges of the anterior margin of the reservoir and may enable the reservoir to be kept in position when its contents are ejected, preventing any tendency of the gland reservoir to evert through the orifice as occurs in *Acrotylus*.

The aorta (AO) travels ventrally to the gland in the mid-line but a slender transparent suspensory filament (SF) leaves it just anterior to the gland and bends round on to the dorsal surface of the gland, finally attaching to the hypodermis of the roof of the pronotum at the posterior sulcus. Ventral to the gland the aorta is flanked by a spongey mass of pericardial cells which contain numerous reflective pink crystals in material which has been fixed in acetic alcohol. The protergal (PT1, PT2) and tergopleural (TP1, TP2) muscles are inserted on the underside of the roof of the pronotum dorsal to the gland (severed in Fig. 2). The dorsal surface of the gland is served by a pair of tracheal trunks, one on each lobe, each with a network of tracheoles. In both O. *senegalensis* and *O. nigeriensis* there are large paired prothoracic air sacs ventral to the gland, and a single median air sac dorsally under the raised median carina of the pronotum.

In *Oedaleus nigeriensis* the gland has not previously been studied. In the nymphal stages it is considerably larger than in *O. senegalensis*, extending posteriorly as far back as the junction between the pterothorax (PT) and abdominal segment I (AB) (Fig. 3). The associated musculature is similar to that in *O. senegalensis*, but the aorta is enveloped in the mesothorax by the two posterior lobes of the gland reservoir which, though seperate, are closely pressed together in the mid-line. There is a large sheet of fat body covering the ventral surface of these lobes and the aorta in the metathorax.

In *Oedaleus senegalensis* the secretion is more readily produced by nymphs than by adults but in *O. nigeriensis* it is impossible to elicit any secretion from adults at all. In the adult *O. nigeriensis* the gland is degenerate (Fig. 4), with its reservoir (GR) reduced to a pair of thin membranous sacs lying along the aorta below the mass of pericardial cells and lacking any associated musculature.

DISCUSSION

The function of VOSSELER's gland is assumed to be repugnatorial. The secretion is a clear greenish fluid, perhaps largely composed of haemolymph, but with a strong and rather unpleasant smell. After expulsion of the fluid the body of a nymph rapidly becomes covered by it and the exhalation of air from the mesothoracic spiracles causes the fluid to froth and assists volatilisation.

However despite the presence of a defensive gland, nymphs and adults of *Oedaleus* are readily taken in the field by a variety of predators (CHEKE, FISHPOOL & FORREST 1980). Any adaptive advantage conferred by the possession of the gland remains unknown.

It would be of considerable interest to determine the chemical structure of the volatile component of the secretion with a view to establishing its function. The secretion can readily be collected direct from the gland by inserting a microcap carefully through the orifice into the reservoir.

It is possible that differences in the development of the gland in *O. senegalensis* and *O. nigeriensis* represent different stages in the evolution of the defensiv use of the gland, perhaps leading to its greater development in and its restriction to the vulnerable nymphal stages of the life cycle where it might be more effective and not liable to foul the wings of the adults. At present this can only be a conjecture.

It would be useful to dissect alcohol-preserved material of other *Oedaleus* species to determine whether there is any relation between the shape of the pronotal hind margin and the development of the gland in adults. *O. senegalensis* has the pronotal hind margin rounded whereas in *O. nigeriensis* it is obtusangular. An angular hind margin might tend to deflect the secretion downwards on to the wing bases. The examination of gland morhology in other *Oedaleus* species would also provide information which could contribute to a reconstruction of the phylogeny of the genus.

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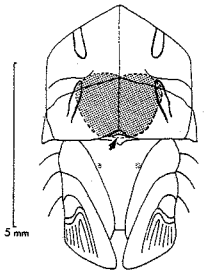
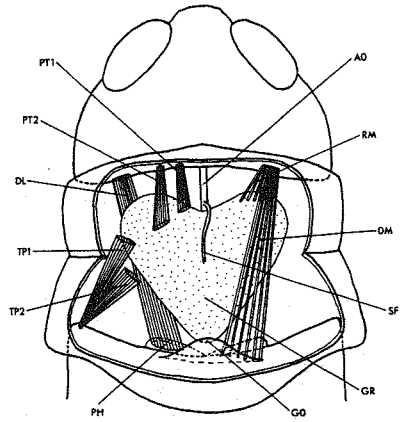


Fig. 1

Thorax of fourth instar nymph of Oedaleus senegalensis (KRAUSS), in postero-dorsal view, indicating position of gland orifice (arrowed) and gland beneath surface of pronotum (stippled).

Fig. 2

Diagrammatic representation of Vosseler's gland and associated structures in fifth instar female nymph of Oedaleus senegalensis (KRAUSS). Dorsal view, with dorsum of pronotum cut away and muscle attachments severed. AO, aorta; DL, dorsal longitudinal muscle; DM, dilator muscle of gland orifice; GR, gland reservoir; PH, phragma; PT1, PT2, protergal muscles of the head; RM, retractor muscle of gland; SF, suspensory filament; TP1, TP2, tergopleural muscles. For clarity all muscles are shown for one side only.



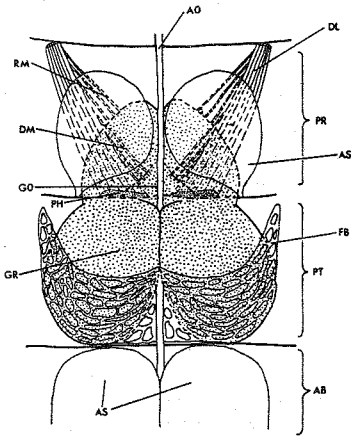


Fig. 3

Diagrammatic representation of Vosseler's gland and associated structures in fourth instar female nymph of Oedaleus nigeriensis Uvarov. Ventral view, with gut removed. AB, abdominal segment I; AO, aorta; AS, air sacs; DL, dorsal longitudinal muscle; DM, dilator muscle of gland orifice; FB, fat body; GO, position of gland orifice (dorsal); GR, gland reservoir; PH, phragma; PR, prothorax; PT, pterothorax; RM, retractor muscle of gland.

Fig. 4

Diagrammatic representation of degenerate Vosseler' s gland of adult female O. nigeriensis UVAROV. Dorsal view. AO, aorta; GR, gland reservoir; PC, pericardial tissue; PH, phragma; PR, prothorax; PT, pterothorax.