

A possible sound producing structure in *Maniola* butterflies (Lepidoptera, Nymphalidae)

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Summary

The Jullien organs of six species of *Maniola* (*jurtina* L., *megala* OBERTHÜR, *chia* THOMSON, *telmessia* ZELLER, *cypricola* GRAVES, *nurag* GHILIANI) were examined by scanning electron microscopy. The surfaces were found to be furnished with tooth-like structures, varying from species to species. It is suggested that the structures may be used in sound production in association with the valve and that they could be of great importance in the evolution of the group. Similar structures in other Lepidoptera are discussed.

Résumé

L'auteur a examiné au microscope électronique à balayage les organes de Jullien de six espèces du genre *Maniola* (*jurtina* L., *megala* OBERTHÜR, *chia* THOMSON, *telmessia* ZELLER, *cypricola* GRAVES, *nurag* GHILIANI). Il a constaté ainsi que leurs surfaces étaient garnies de structures dentées qui varient d'une espèce à l'autre. Il suggère que ces structures pourraient être utilisées à la production de sons, en combinaison avec les valves, et qu'elles pourraient avoir une grande importance dans l'évolution du groupe. Des structures similaires chez d'autres espèces de Lépidoptères sont évoquées.

In the course of a survey of morphological characters of butterflies belonging to the Satyrine tribe Maniolini, the 'Jullien organ' of butterflies of the Satyrine genus *Maniola* was examined (THOMSON, 1987a). This structure, which is present in males only, comprises a series of hard, black chitinous rods fused together in bundles attached to both sides of the last (eighth) abdominal tergite. They are not found in any other Manioline genus. Corresponding structures are found in several other Satyrids and their morphology has been used in the identification of certain *Hipparchia* species (KUDRNA, 1977 ; COUTSIS, 1983(84) ; LERAUT, 1990). Similar external features occur outwith the

family (REVERDIN, 1915), including *Hamadryas* (*Ageronia* s.l.) and the Nearctic Sphingid moths of the genus *Psilogramma* (ROBINSON & ROBINSON, 1972 ; LLOYD, 1974).

In his little known paper, REVERDIN observes :

‘... I have read a remark by Fritz Muller incorporated in Dr G. B. Longstaff’s work. “Just as the *Ageronia* ... only make the remarkable crackling sound on the wing and during courtship, so also, in all probability, butterflies equipped with brands, tufts, etc., only distribute their scent under the same circumstances.” May we not deduce that this crackling sound is caused by the friction of the spiculae against another part of the genitalia, and that the Jullien organ has the same function, the action being modified by their situation ; it would seem as though the motionless organ of *Ageronia* were rubbed by the mobile valves, whereas the mobile spiculae of the Jullien organ in *Satyrus* [and *jurtina*] rub against the valves or uncus...’

The surface topography of the rods unexpectedly proved to be very much more interesting. It was found to be irregularly fluted, varying from species to species, and, most interestingly of all, furnished with an extremely complex pattern of teeth, reminiscent of some stridulatory organs in Orthoptera (Figures 1-3).

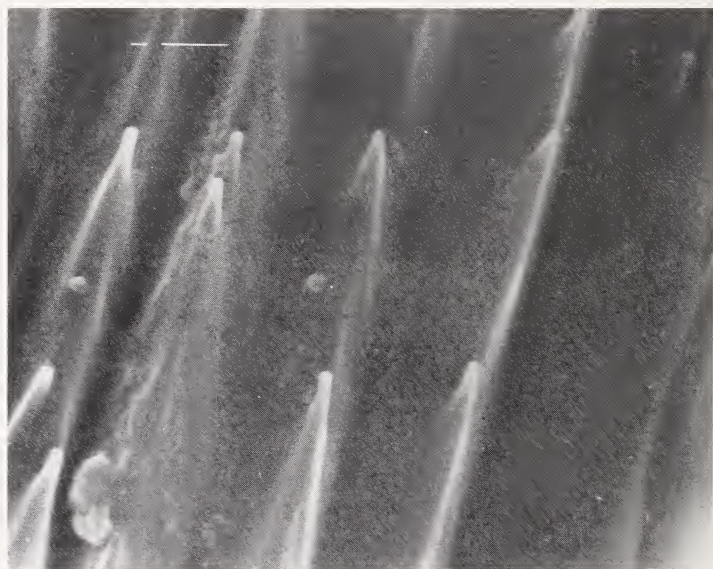


Fig. 1. Jullien organ of *Maniola jurtina*, Scotland, X9700, SEM0468/1.



Fig. 2. Jullien organ of *Maniola chia*, Chios, X9200, SEM0620/8.

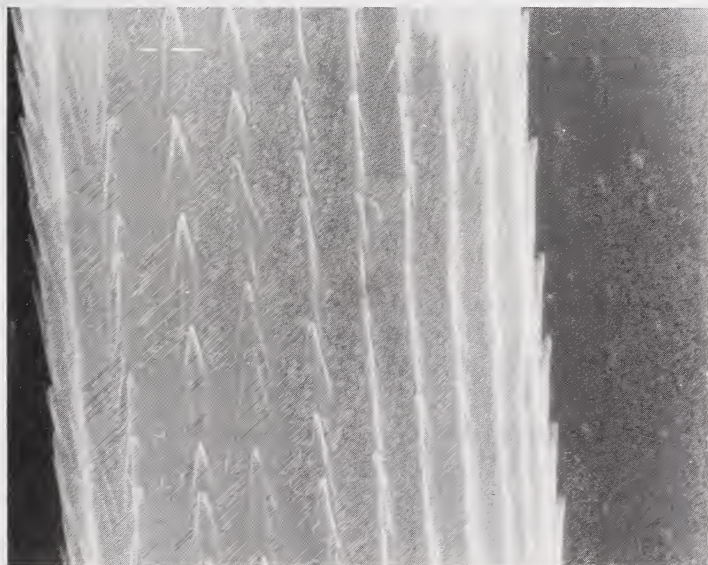


Fig. 3. Jullien organ of *Maniola telmessia*, Rhodes, X9500, SEM0460/1.

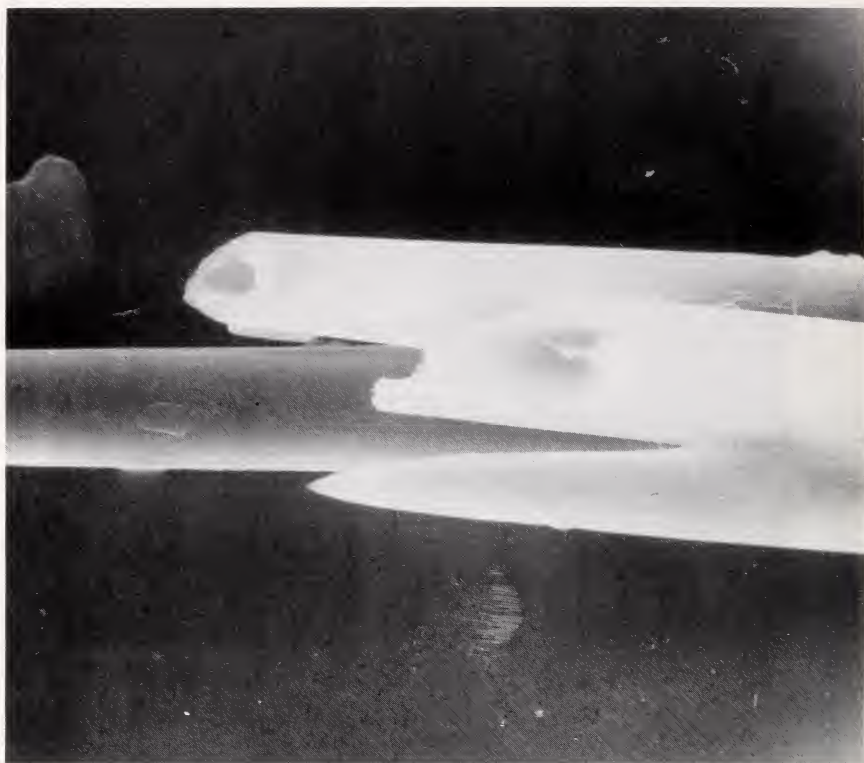


Fig. 4. Jullien organ of *Maniola nurag*, Sardinia, showing hollow rod structure, X900, SEM0443/6.

Methods and materials

All specimens were mounted using double-sided adhesive tape and coated lightly with gold using an Edwards S150 sputter coater. SEM work was undertaken on an ISI-60A instrument. All images were generated at 2.5 to 4kV.

Ten specimens each of the six *Maniola* species were examined by scanning electron microscopy at high magnification, *jurtina* L. (1758) from the Canary Islands and Scotland, *megala* OBERTHÜR (1909) from Turkey, *chia* THOMSON (1987) from Chios, Greece, *telmessia* ZELLER (1847) from Lebanon and Rhodes, *cypricola* GRAVES (1928) from Cyprus and *nurag* GHILIANI (1852) from Sardinia.

Results

There are some differences in the gross morphology of these structures between *Maniola* species. The Jullien organ of *telmessia*, *cypricola* and *nurag* is formed of fewer rods than that of *jurtina*. Examination of *chia* and *megala* indicated that their organs had an affinity with *jurtina*, being strong and formed of many rods, although in *chia* this characteristic was a little less pronounced. Using scanning electron microscopy, the ultrastructure of the Jullien organ was examined in detail. It was found to be a set of hollow tubes, with no external punctures or openings (Figure 2). From these initial observations it was concluded that earlier suggestions (REVERDIN, op. cit.) that the organ was for scent production were highly improbable, although they did not eliminate the possibility, which was also JULLIEN's own belief, that they were of a 'tactile order'.

Some general observations can be summarised.

1. The fluting varies to some extent from rod to rod, but the height of the ridges (or depth of valleys) is similar within species and varies greatly between species.
2. The extent and location of teeth is characteristic of each species. In some *Maniola*, the teeth are similar on the inner and outer external surfaces of the Jullien organs, while in others they are restricted to specific areas of the inner surfaces.
3. Interspecific differences were noted in the frequency and length of teeth within the toothed area. No teeth were detected in *megala*.
4. The distance between teeth is fairly constant in some parts of the organ and irregular in others. There are considerable differences in the degree of teeth regularity between species.

The characteristics of the Jullien organs in *Maniola* are detailed in Table 1.

Table 1. Ultrastructural characteristics of the Jullien organ of *Maniola* species.

species	fluting/ ridge heights	teeth length	teeth frequency	teeth regularity
<i>jurtina</i>	fine/high	short	variable	irregular
<i>megala</i>	v.fine/high	? absent	-	—
<i>chia</i>	coarse/f.high	short	frequent	irregular
<i>telmessia</i>	coarse/low	long	frequent	regular
<i>cypricola</i>	coarse/low	short	frequent	irregular
<i>nurag</i>	coarse/low	v.long	frequent	regular

Discussion

The seventh, eighth and ninth intersegmental regions of the male abdomen are known frequently to be connected with display, scent-producing and scent-distributing structures consisting of pouches and supports for eversible and erectile masses of modified hairs or scales (KLOTS, 1970). The suggestion that these structures were sound generators, made by REVERDIN, was with reference to similar structures (the 'Godman and Salvin organ') in the south American Nymphalid genus *Hamadryas* (= *Ageronia*), known popularly as 'crackers' because of the sounds they make. However, in this group the organ is inserted in the upper edge of the ventral portion of the terminal segment (sternite) of the abdomen, not in the eighth segmental tergite as in *Maniola*. These organs in *Hamadryas* possess 'hairs' or spiculae varying in number and length, yet REVERDIN is the only author to associate these structures with the butterflies' auditory generation (FRUHSTORFER, 1924 ; EHRLICH & EHRLICH, 1961 ; ROSS, 1963 ; SWIHART, 1967). Adult acoustic signaling is known in only a few other butterflies, eg *Neptis hylas* (SCOTT, 1968) and a Neotropical Satyrine species tentatively identified as '*Pharneuptychia* nr. *pharnabazos*' (KANE, 1982).

It is more likely that the Manioline Jullien organs correspond functionally with the eighth tergite spines in *Psilogramma* moths. The ventral surfaces of the genital valves in species of that genus are furnished with 'plectrum scales', presumed to be used in sound generation. ROBINSON & ROBINSON (1972) suggest that the valves strike the spines and that each oscilloscope beam deflection which they recorded represented a spine-scale impact. However, LLOYD (1974) points out that the sounds are too complex for this to be the case.

The observations described here strengthen the hypothesis that the Jullien organ in *Maniola* has a sound producing function. If this is so, the most likely structure which would complete the mechanism would be the genital valves. Characters of the male genitalia within Maniolini are distinctive. Much information of evolutionary significance can be deduced from the shape and form of the valve in the group. In *Hyponephele*, *Cercyonis*, *Pyronia* and *Aphantopus* the valve is long, narrow and tapering. *Maniola* is distinct in being the only genus in which the valves are broad. Their form is quite unlike that of the other genera and far more divergent that would be expected from its relatively close relationship with the other Maniolini. Geographical variation is notable in both male and female armatures in *Maniola jurtina* (HIGGINS, 1975 ; THOMSON, 1973, 1976). Similar patterns of geogra-

phical variation have not been noted in other *Maniola* species, although it is possible that they exist.

It is significant, perhaps, that those of *Maniola* are unique in Maniolini in being broad in form. Indeed, broad shaped valves are rare in the Satyridae (HIGGINS, 1975). It is interesting also that the shape of the dorsal process of the valve is characteristic of *Maniola* species (THOMSON, 1973, 1976, 1987a). Examination of living *jurtina* reveals that the juxtaposition of the Jullien organ and the dorsal process would facilitate stridulation : both structures can be manipulated independently by the insects. The hollow form of the rods might amplify any sound produced by the valve rubbing against the Jullien organ. Unfortunately, the evidence, at present, is still circumstantial.

No *Maniola* has been heard to make a sound. Initial attempts to detect and record sounds from these butterflies have so far failed. The sounds thus generated might well be beyond our hearing capabilities (about 8kHz maximum) and ultra-sonic detecting apparatus (a sonagraph with wide band filter settings) would be required. It is known that the range of auditory perception in insects, especially Lepidoptera, extends into frequencies far beyond those which the human ear can detect (WIGGLESWORTH, 1974). The sound spectrogram from *pharnabazos* (KANE, 1982) illustrates that most of the sounds which this species generates are ultrasonic.

If the Jullien organ in *Maniola* is a stridulation organ, as these ultra-structural studies would suggest, it could be of considerable importance, as a reproductive isolating mechanism, to evolutionary studies of the genus. The different tooth patterns observed in the various species could give rise to species-specific sound patterns, could be vitally important in mate location and/or stimulation and, more importantly, it could act as a mode of species consolidation accelerating the speciation process through very acute selection pressures.

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