

Ovipositor Steering Mechanisms in Braconid Wasps

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Abstract.—Ovipositor features which allow the ovipositor tip to be manipulated and which have restricted distributions among the subfamilies of Braconidae are described and illustrated for the first time. Members of the Amicrocentrinae, Charmontinae, Helconinae and Macrocentrinae have the rhachis (the tongue-like part of the mechanism that interlocks the upper valve with the lower ones) with an increased density of scale-like sculpture and often also swollen pre-apically. This modification leads to increased friction and restricted movement between the upper and lower valves and is also associated with an ovipositor bending mechanism in which retraction of the lower ovipositor valves relative to the upper one causes the ovipositor tip to bend ventrally. Many members of the subfamilies Agathidinae and Orgilinae possess a pair of pre-apical boss-like projections on the upper ovipositor valve (gonapophyses 9) and a corresponding structure on each lower valve (gonapophyses 8) that together enable the wasps to bend and manipulate the ovipositor apex by retraction of the lower ovipositor valves relative to the upper one. Most members of the Doryctinae have the aulax (the groove-like part of the mechanism that interlocks the lower valve with the upper one) constricted opposite modified pre-apical, dorso-lateral tooth-like structures. These constrictions restrict the relative movement between the upper and lower valves and thus operate as an ovipositor bending mechanism. The potential phylogenetic significance of these mechanisms is discussed, and preliminary parsimony analyses are described which suggest that the pre-apical boss-like projections of the Agathidinae and Orgilinae may represent a synapomorphy uniting these two subfamilies.

INTRODUCTION

Oviposition behaviour and, as a consequence, the ovipositor have been of immense importance in the evolution of the Hymenoptera, and are central to the parasitic way of life (Gauld & Bolton 1988). The commonly held view that the ovipositors of parasitic wasps are fairly simple analogues of hypodermic needles is therefore likely to be a considerable over-simplification as has in fact been shown by several previous investigations of functional morphology (Oeser 1961; Austin & Browning 1981; Quicke et al. 1992a,b, 1994).

Several braconid genera have recently been shown to possess highly modified

ovipositors whose tips are capable of being independently actively manipulated by the wasp even though the ovipositor valves themselves are devoid of intrinsic musculature and their relative movements are controlled by muscles within the metasoma. Mechanisms, as found for example in the braconine genus *Zaglyptogastra* Ashmead, were apparent because of very conspicuous features of the intact ovipositor (Quicke 1991; Quicke & Marsh 1992). However, an ability to manipulate or steer the ovipositor tip has been observed in a number of other parasitic Hymenoptera whose ovipositors appear more or less unmodified externally (Delanoue & Arambourg 1965; Compton & Nefdt 1988). Further, our own observations have also

shown that an ability to manipulate the ovipositor tip is present in members of several subfamilies of Braconidae that possess moderately long ovipositors. We have therefore examined ovipositor tip structure in detail across a range of braconid taxa. Here we describe three different types of morphological specialisation found in the Braconidae that appear to underlie the manipulatory abilities observed. These modifications all utilise the same mechanical principle but they achieve this through modification of different structures. In these cases, the structures involved can often only be revealed by examination of separated ovipositor valves using scanning electron microscopy; however, their existence supports the view that the ovipositors of parasitic wasps are highly specialised and complex structures.

Two different ovipositor steering mechanisms, one involving a sinuous apical region of the ovipositor the other involving the development of an aulaciform rod between the largely separated halves of the upper ovipositor valve have been reported previously (Quicke 1991; Quicke et al. 1994). The first of these is possessed by several unrelated taxa of Braconidae and Ichneumonidae, the second so far is known only from members of the Ichneumonidae. During investigations of ovipositors belonging to a large number of other ichneumonid wasps collectively representing most subfamilies, no steering specialisations similar to any of the three described here for Braconidae have been detected. Functionally similar but morphologically different mechanisms in members of two other families of parasitic Hymenoptera, Gasteruptiidae and Aulacidae, are being described elsewhere (Quicke & Fitton, in press).

GENERAL MORPHOLOGY

The ovipositors of Hymenoptera are comprised of components that are believed to be derived primitively from two pairs of metasomal appendages (Smith

1968, 1970). The two gonapophyses of abdominal segment 9 are usually fused along their length and form the single upper valve, while those of segment 8 remain separate and form the two lower valves. The upper valve is interlocked with each lower valve by a longitudinal tongue and groove joint referred to as the olistheter. The tongue or rhachis situated ventro-laterally on each side of the upper valve is 'T'-shaped in transverse section and in life runs within the 'T'-shaped groove or aulax on the dorso-lateral face of the lower valve (Fig. 1).

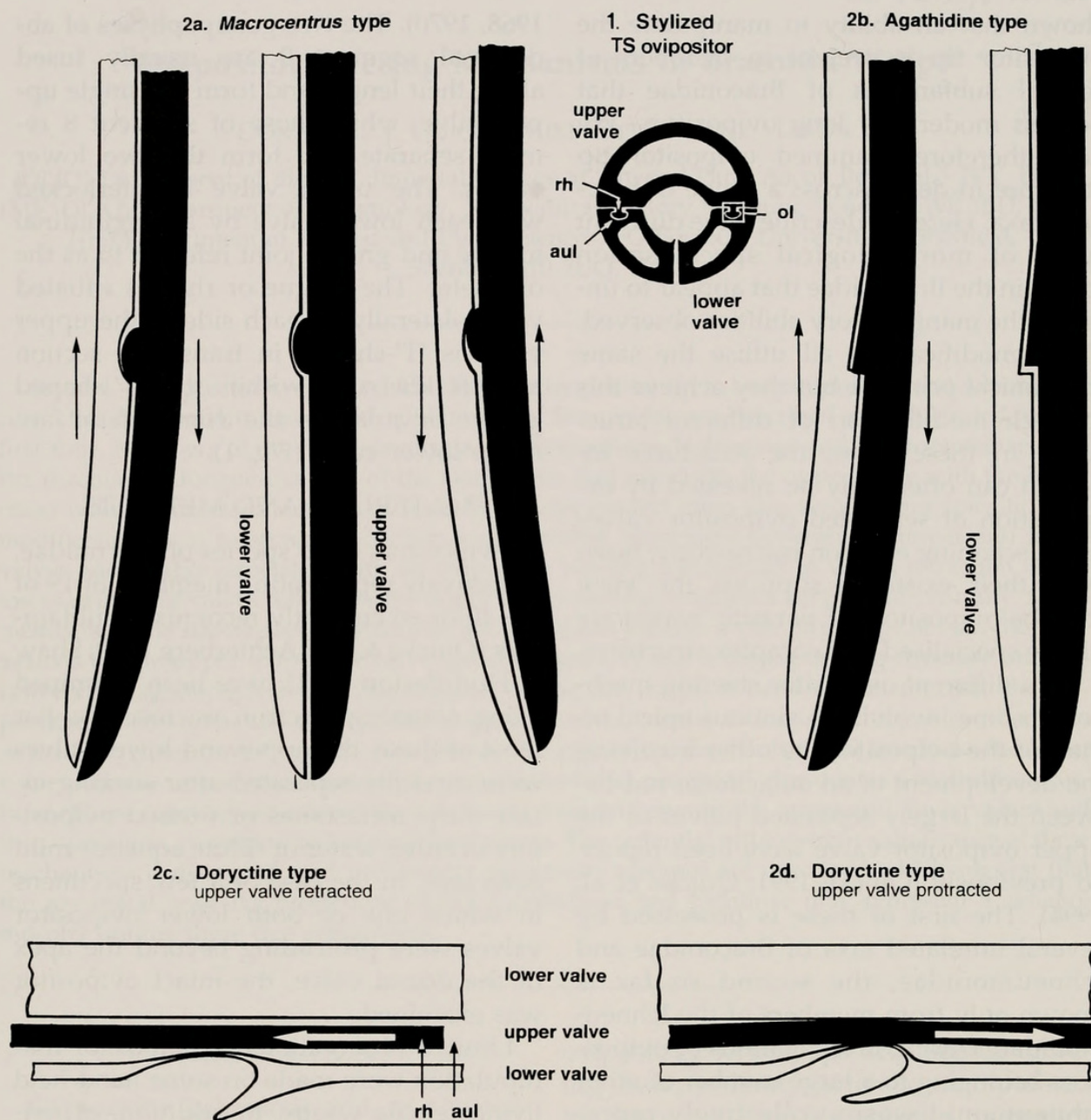
MATERIALS AND METHODS

Ovipositors of 70 species of Braconidae, collectively representing members of 19 of the 40-or-so currently recognised subfamilies (Quicke & van Achterberg 1990; Shaw & Huddleston 1991) have been examined using scanning electron microscopy. For most of these, the upper and lower valves were carefully separated after soaking intact wasp metasomas or excised ovipositors in either water or dilute aqueous mild detergent. In the case of a few specimens in which one or both lower ovipositor valves were protruding beyond the apex of the dorsal valve, the intact ovipositor was examined.

Limited observations of ovipositor manipulation were made on some hand-held living female wasps. In addition, experiments were carried out using excised ovipositors from freshly killed wasps. Ovipositors were submerged under water and the effects observed of pulling and pushing the cut ends of the basal portions of the upper and lower valves differentially with fine forceps.

The taxa investigated are listed below according to subfamily. Where more than one individual of a species was examined the number is given in parentheses.

Agathidinae: *Braunsia* sp., Cameroun (3); *Camptothlipsis* sp., Kenya; *Megagathis* sp., Sierra Leone; *Microdus rufipes* Nees, UK. Alysiinae: *Phaenocarpa conspurcator*



Figs. 1, 2. 1. Diagrammatic transverse section (TS) through mid-region of braconid ovipositor to show olistheter mechanism: (ol) olistheter, (rh) rhachis, (aul) aulax. 2. Diagrammatic representations of how the three ovipositor bending mechanisms are believed to operate. a, Macrocentrinae, Amicrocentrinae, and Charmontinae, lateral views showing preapical swelling of rhachis; b, Agathidinae and Orgilinae, lateral views showing pre-apical bosses; c, d, Doryctinae, dorsal showing in the postulated increased grip against the rhachis when the upper valve is protracted.

(Haliday), Netherlands. Amicrocentrinae: *Amicrocentrum* sp., Tanzania. Blacinae: *Artiocus spinarius* Achterberg, Brazil (2); *Blacus hastatus* Haliday, Sweden; *B. longipennis* (Gravenhorst), UK; *B. maculipes* Wesmael, Austria; *B. nigricornis* Haeselbarth, UK; *B. paganus* Haliday, UK; *B. pallipes* Haliday, UK; *B. ruficornis* Nees, Hungary,

Russia (2); *Dyscoletes lancifer* (Haliday), UK, Germany (2). Braconinae: *Digonogastrea* sp., Trinidad; *Euurobracon yokahamae* Dalla Torre, Japan; *Glyptomorpha* sp., Gambia; *Nesaulax* sp., Papua New Guinea; *Odesia* sp., Kenya; *Virgulibracon endoxylaphagus* Quicke & Ingram, Australia. Cardiochilinae: *Cardiochiles* sp., Cameroun. Cen-

ocoeliinae: *Capitoniuss* spp., Brazil (2). Charmontinae: *Charmon cruentatus* Haliday, UK (2). Doryctinae: *Acanthodoryctes tomentosa* (Szépligeti), Australia; *Acrophasmus ferrugineus* (Marsh), USA; *Allorhogas pyralophagus* Marsh, Trinidad; *Binarea* sp., Argentina; *Doryctes erythromeles* (Brullé), USA; *Liobracon* sp., Brazil; *Megaloproctus platyantennus* Marsh, Brazil; *Monarea* sp., Brazil; *Rhaconotus* sp., USA; *Rutheia* sp., Bolivia; *Syngaster* sp., Australia; *Spathius* sp., Kenya; *Zombrus* sp., Kenya. Helconinae: *Austrohelcon* sp., Australia; *Aspicolpus carinator* Nees, Hungary; *Aspidocolpus* sp., Nigeria; *Baecis abietis* (Ratzeburg), Poland; *Brulleia latiannulatus* (Cameron), New Guinea; *Calohelcon obscuripennis* Turner, Australia; *Diospilus capito* (Nees), Hungary (2); *Diospilus morosus* Reinhard, Austria; *Eubazus pallipes* Nees, Romania; *E. tibialis* Haliday, Bulgaria; *E. (Brachistes)* spp., Argentina, UK (2); *Helcon nunciator* Fabricius, Hungary; *Helconidea tentator* (Fabricius), Belgium; *Polydegmon sinuatus* Foerster, Hungary; *Taphaeus hiator* Thunberg, Hungary; *Wroughtonia* sp., Canada; undescribed genus A, Australia; undescribed genus B, Australia. Homolobinae: *Homolobus truncator* (Say), Bulgaria (2); *H. (Oulophus)* sp., USA. Macrocentrinae: *Austrozele uniformis* Provancher, USA; *Macrocentrus linearis* Nees, Hungary (2); *Macrocentrus* sp., Poland. Microgastrinae: *Sathon falcatus* (Nees), Germany. Microtypinae: *Microtypus* sp., Hungary. Opiinae: *Doryctobracon* sp., Trinidad. Orgilinae: *Orgilus leptcephalus* (Hartig), Germany; *Orgilus* spp., Cameroun, France (3); *Orgilonia* sp., Cameroun; *Stantonina* sp., Cameroun. Pamolininae: *Monitoriella elongata* Hedqvist, USA. Pselaphaninae: *Pselaphanus trogoides* Szépligeti, Surinam. Rhysipolinae: *Rhysipolis* sp., UK

RESULTS

Upper Valve Rhachis Scaling and Expansions

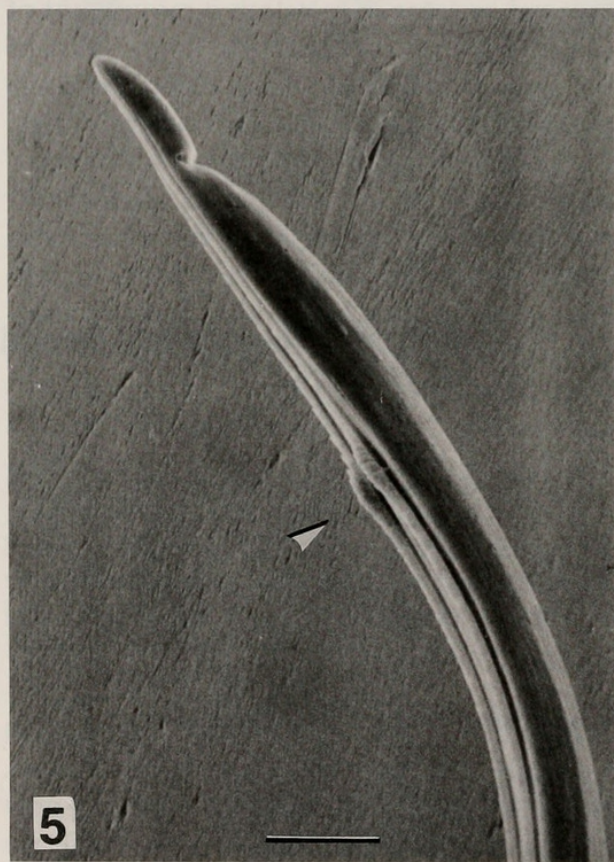
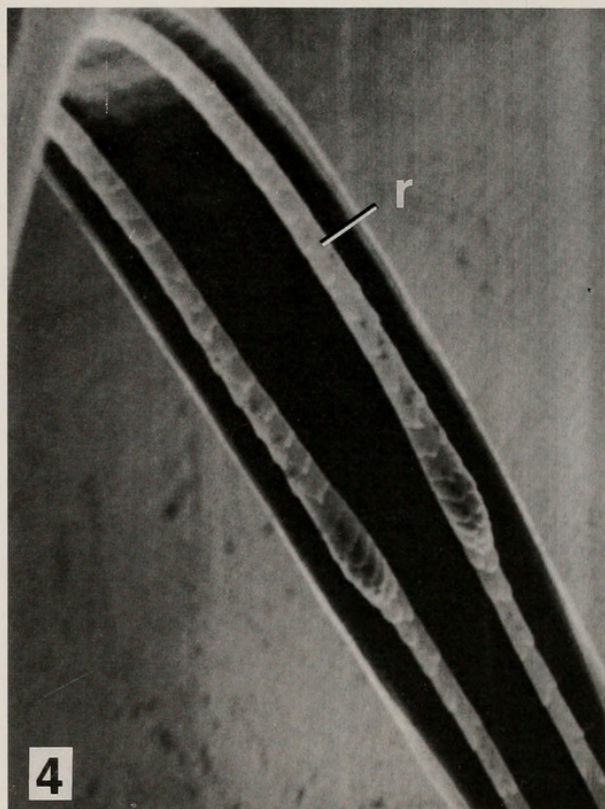
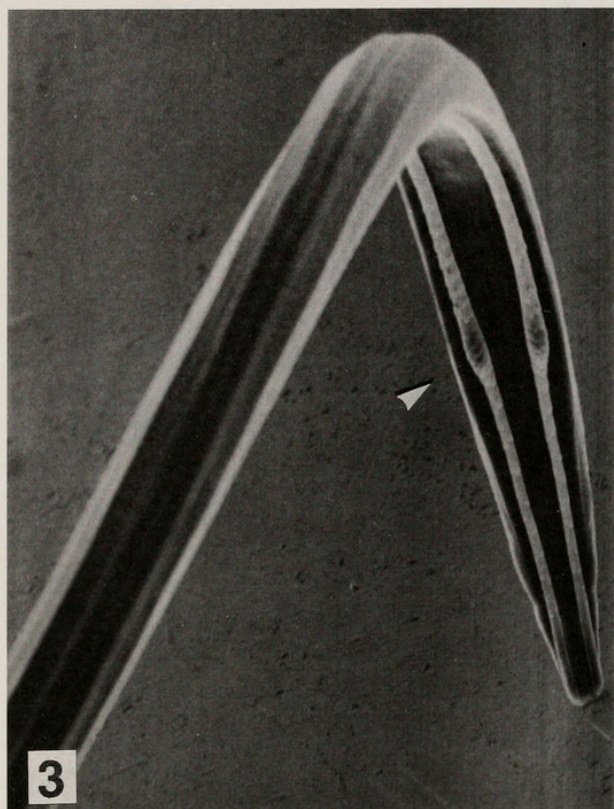
In all Hymenoptera both the rhachis and the margins of the aulax are furnished

with scale-like sculpture which, in the case of the parasitic Apocrita and the Orussidae, are generally rather widely spaced (Figs. 16, 17). In the Amicrocentrinae, Blacinae, Charmontinae and Helconinae the density of scaling was found to be considerably increased over a short region preapically (Figs. 3–11). Further, in the Charmontinae and Macrocentrinae this is accompanied by a distinct swelling of the rhachis (Figs. 3–6; arrowed) and slight widening of the corresponding length of the aulax.

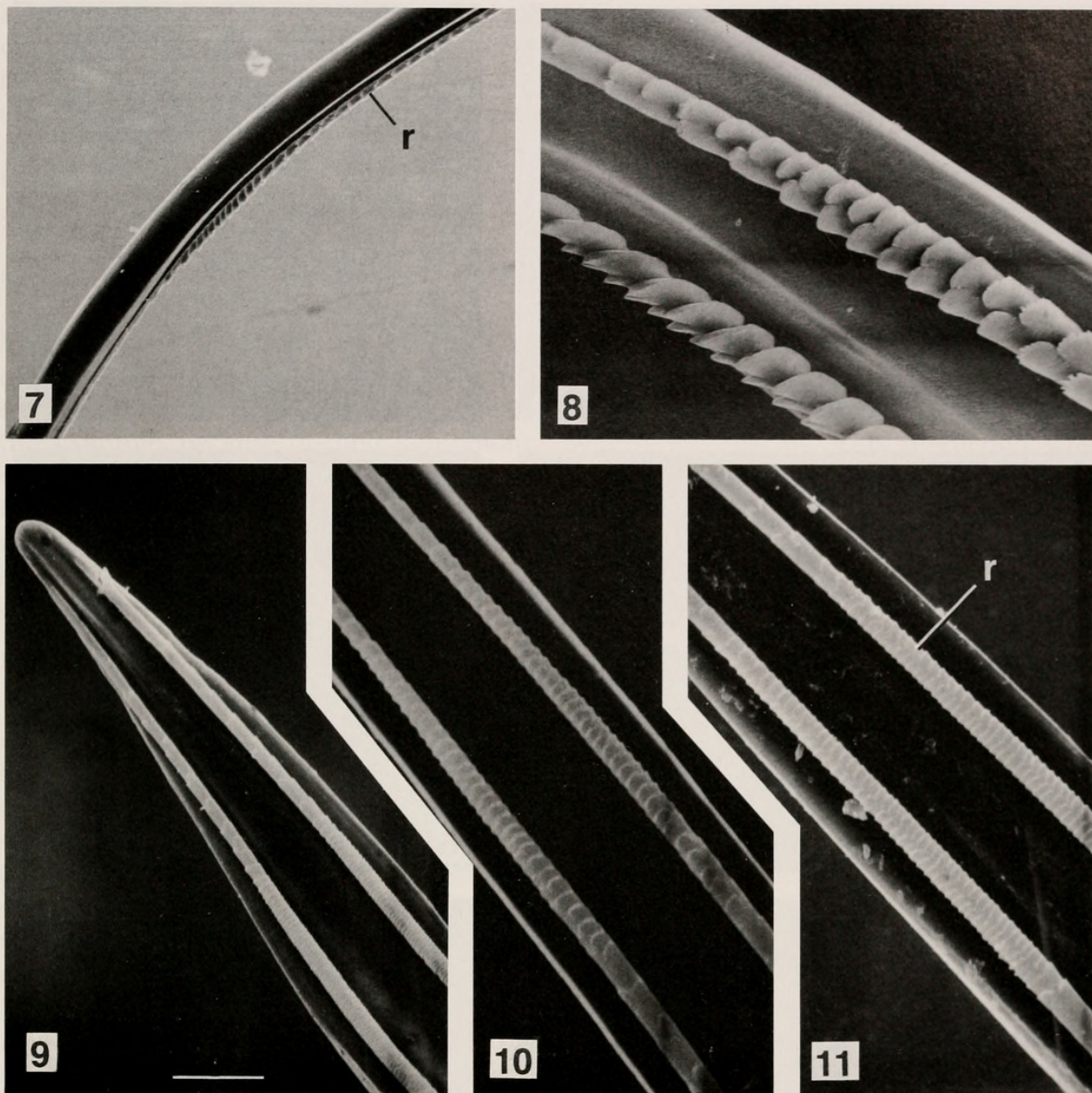
Observation of living *Macrocentrus* females held in the hand showed that they are capable of bending the apex of their ovipositors ventrally through nearly 90°. It seems likely that this is achieved in an analogous way to that proposed for the Agathidinae and Orgilinae (see below), with the swollen and more coarsely sculptured region of the rhachis providing increased resistance to relative movement of the ovipositor valves at the apical part of the ovipositor. Thus, if the dorsal valve is protracted relative to the ventral ones, they will not be able to slide past one another freely at the apex, and so the ovipositor will be forced to curve ventrally in order to accommodate the relative extension of the upper valve in a manner analogous to the bending of a bimetal strip in a thermostat, as illustrated diagrammatically in Fig. 2a. The plausibility of this was conclusion was substantiated by manipulation of the cut ends of an excised *Macrocentrus* ovipositor which showed that protraction of the upper valve relative to the lower one causes a ventral curving of the ovipositor tip.

Upper and Lower Valve Bosses

In all members of the Orgilinae and most Agathidinae examined, the pre-apical lateral margins of both the upper (Figs. 12, 13, 16, 17) and lower (Figs. 14, 15) ovipositor valves possess an abrupt escarpment-like boss in lateral aspect. These structures are located lateral to the olis-



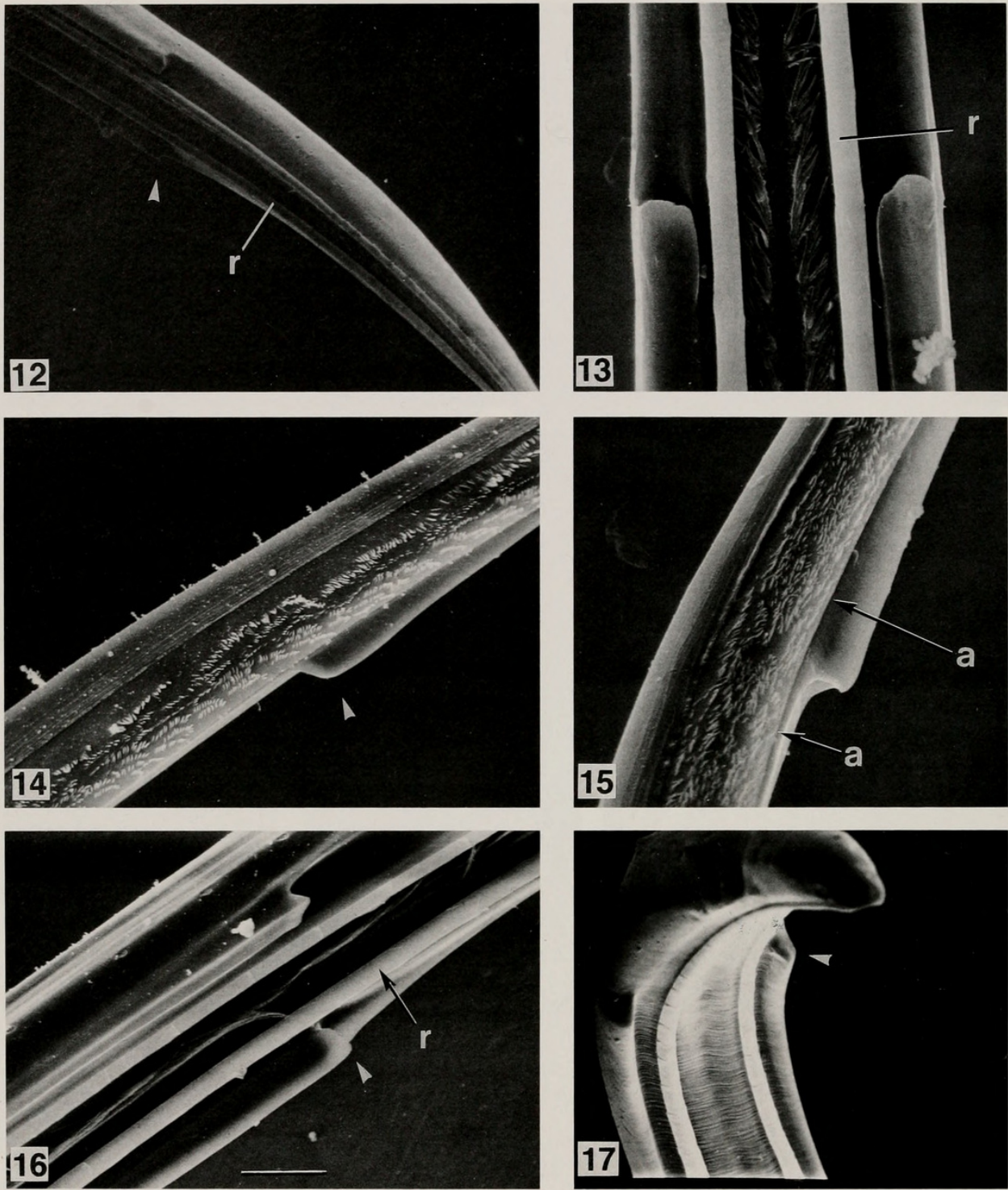
Figs. 3–6. Scanning electron micrographs of apical parts of isolated upper ovipositor valves showing preapical expansion of rhachis (r) with denser scaling (arrows). 3, 4 (detail), *Charmon cruentatus*. 5, *Macrocentrus linearis*. 6, *Macrocentrus* sp. Scale line: 3, 5: 50 μ m; 4, 6: 25 μ m.



Figs. 7–11. Scanning electron micrographs of apical parts of isolated upper ovipositor valves showing weak preapical expansion of rhachis (r) with denser scaling (arrows). 7, 8, *Amicrocentrum* sp. 9, *Helconidea tentator*. 10, *Wroughtonia* sp. 11, *Brulleia latiannulatus*. Scale line: 7: 100 μ m; 8: 20 μ m; 9, 50 μ m; 10, 11: 40 μ m.

theter. In the case of the dorsal valve, the steep (scarp) face of the stop is at the distal end of the modified region whereas it is at the proximal end in the lower valve. The positioning of these modifications is such that when the ovipositor is in its resting position with neither upper nor lower valves apically protruding beyond the other, the scarp faces of both processes are closely apposed. The presence of these stops limits the relative longitudinal

movement of the upper and lower valves such that the upper valve cannot be protracted apically, relative to the lower valves, beyond the resting position though the upper valve can be retracted basally. The functional significance of this modification was revealed when living agathidines of the genus *Agathis* were held in the hand and the apical part of the ovipositor was observed to change its degree of ventral curvature as the wasp attempted to



Figs. 12–17. Scanning electron micrographs of apical parts of isolated upper (12, 13, 16, 17) and lower ovipositor valves (14, 15) showing (arrows) corresponding preapical, bosses lateral to the rhachis (r) and aulax (a) of the upper and lower valves respectively. 12, 13, 15, *Braunsia* sp. 14, 16, *Megagathis* sp. 17, *Orgilonia* sp. Scale line: 12: 50µm; 13, 16: 20µm; 14, 15: 30µm; 17: 35µm.

free itself. Such bending appeared to be achieved by the wasp protracting the upper valve posteriorly relative to the lower valves, thereby forcing together the op-

posing scarp faces of their bosses. Because the valves are interlocked along their whole length by the olistheter mechanism, the ovipositor is forced to curve ventrally,

as illustrated in Figure 2b. The plausibility of this was concluded was substantiated by manipulation of the cut ends of an excised *Agathis* ovipositor which showed that protraction of the upper valve relative to the lower one causes a ventral curving of the ovipositor tip.

No other braconids examined possessed this modification and since neither the Agathidinae nor the Orgilinae are likely to be the most basal of extant braconids (Quicke & van Achterberg 1990; Wharton et al. 1992; van Achterberg & Quicke 1992) (for example, because of their koinobiont endoparasitoid life history), it seems likely that the presence of a scarp-like stop mechanism is apomorphic. The potential implications of this are dealt with in the discussion.

Pre-apical Constrictions of the Aulax

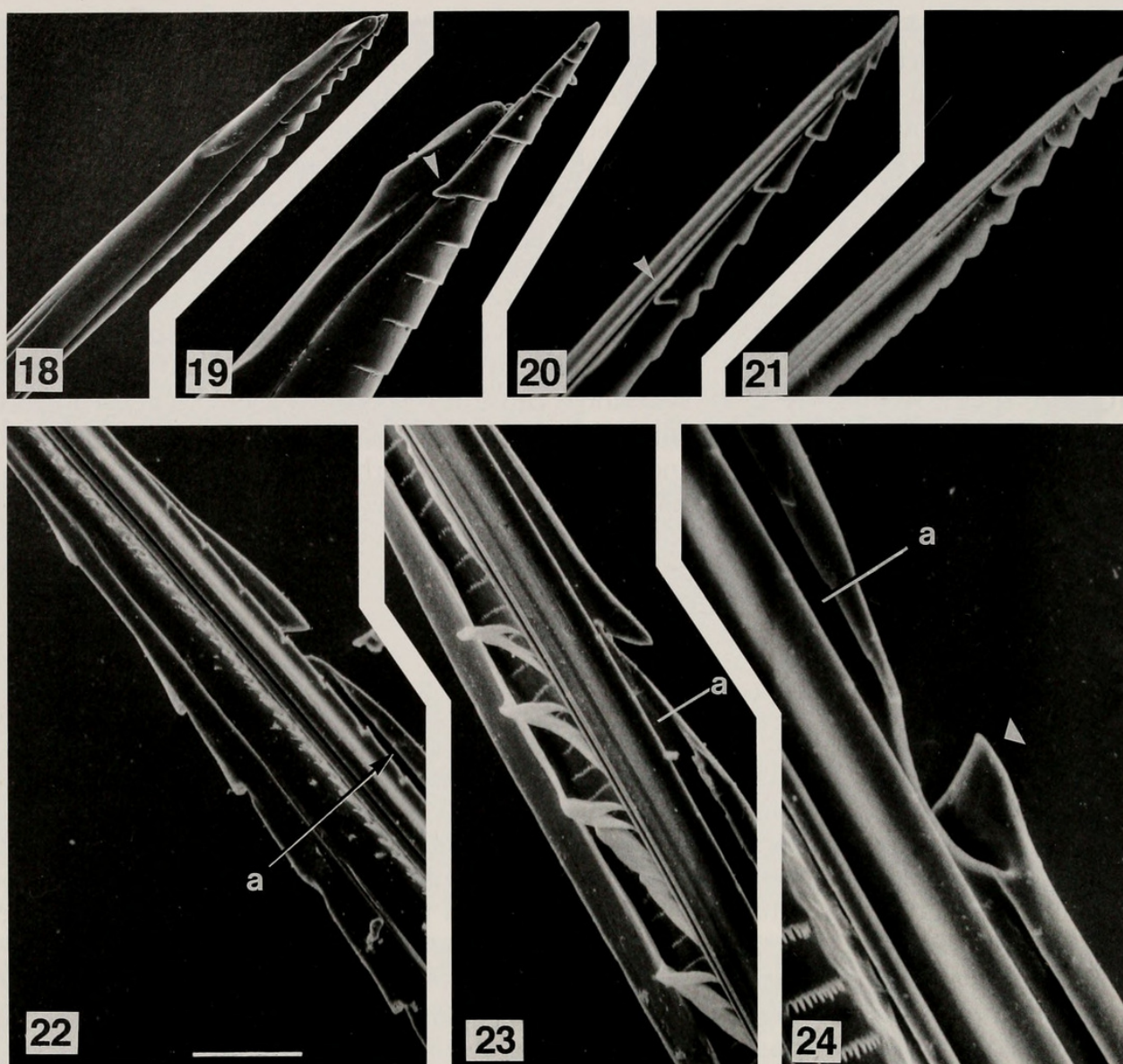
Unlike other braconid subfamilies, most members of the subfamily Doryctinae have the apex of the ovipositor much darker (piceous or black) and much more strongly sclerotized than the remainder (Quicke et al. 1992a) such that it is usually extremely difficult to separate the valves for study even after softening in aqueous potassium hydroxide; though with persistent manipulation, the three parts could usually be separated. Scanning electron microscopy shows that in many genera (e.g. *Binarea*, *Liobracon*, *Monarea*, *Syngaster*, *Zombrus*) the apical part of the lower valves, as well as having ventro-lateral serrations, also possess one or two apparently distinct dorso-lateral tooth-like structures (Figs. 18–21; arrows) (Quicke et al. 1992a). The significance of these in terms of ovipositor steering has been revealed by examination of the adjacent part of the aulax. The aulax is an approximately parallel-sided groove along most of its length, in isolated ventral valves it is strongly constricted opposite these additional teeth by an infolding of the lateral margin (Figs. 22–24). Together with the increased sclerotization of the ovipositor tip

and our observation that it is very difficult to separate the dorsal and ventral valves at the tip region, we conclude that the narrowed region of the aulax acts to grip the rhachis tightly, thereby reducing the freedom of movement of the valves near to the ovipositor tip. The asymmetric arrangement of the constrictions of the aulax are such that retraction of the upper valves is likely to afford less resistance than protraction (Figs. 2c cf d) which will cause the lateral wall of the aulax to roll inwards thus increasing the friction against the rhachis. This prediction was borne out by observations of living *Hecabolus* females which were found to be able to bend their ovipositors ventrally but not dorsally.

DISCUSSION

In all the cases in which we have found to possess probable ovipositor steering mechanisms, their hosts are concealed insect larvae. Orgilines mostly attack weakly concealed hosts such as leaf miners, and they probe into their hosts' tunnels often through frass holes rather than by boring directly through the plant material (Flanders & Oatman 1982; Shaw & Huddleston 1991). Agathidines, charmontines and macrocentrines similarly attack weakly concealed hosts such as leaf rollers, leaf tiers, shoot borers, and, particularly in the case of the Agathidinae, leaf miners/tunnellers. The steering mechanisms may therefore enable the wasps to locate their hosts better within their concealed feeding places. It may also enable the wasps to place their eggs accurately on or within their hosts. In the case of agathidines, for example, it is known that eggs are usually placed very precisely within or next to the host's central nervous system (references in Shaw & Huddleston 1991). Given that their hosts are concealed and often relatively small, such accurate egg placement would be facilitated by the existence of some sort of directional control of the ovipositor tip.

In contrast to the above mentioned sub-



Figs. 18–24. Scanning electron micrographs of apical parts of intact ovipositors (18, 19) and isolated lower ovipositor valves (20–24) of doryctine braconids showing dorso-lateral tooth like structures (arrow) and in 24, the corresponding narrowing of the aulax (a). 18, *Megaloproctus platyantennus*. 19, 24, *Binarea* sp. 20, *Acrophasmus ferrugineus*. 21, *Spathius* sp. 22, *Syngaster* sp. 23, *Zombrus* sp. Scale line: 18: 130 μ m; 19: 70 μ m; 20, 21: 60 μ m; 22, 23: 30 μ m; 24: 10 μ m.

families, many members of the Doryctinae attack more strongly concealed insects such as wood-boring beetle larvae, and since they are idiobiont ectoparasitoids, the exact placement of the paralysing sting or of the egg is usually likely to be of little importance. The process of boring through bark or other hard substrates may not be very accurate and is also quite time consuming, which in turn probably places the wasp under an increased risk of pre-

dation. Locating a host tunnel might therefore be a good first step towards reaching a host if the wasp can subsequently manipulate its ovipositor tip. Steering mechanisms might be seen in these cases as an adaptation which overcomes some of the potential problems of reaching a concealed host directly through a thick layer of substrate.

Of some surprise was that we failed to find any morphological modifications that

could be involved in ovipositor steering in a number of taxa with long to very long ovipositors such as members of the braconine genera *Archibracon*, *Euurobracon*, *Glyptomorpha*, *Nesaulax*, *Odesia* and *Virgilibracon*. Nor were any steering mechanisms identified in the Alysinae, Cardiochilinae, or Cenocoeliinae examined. Observations of living females of these taxa would be valuable as it is quite possible that they have some other, perhaps less conspicuous, mechanisms that enable them to manipulate their ovipositors or ovipositor tips. Certainly for many of the braconines with long ovipositors, oviposition involves boring through hard wood (van Achterberg 1986) and this may pose limitations on the bending mechanisms they might possess. Alternatively, it may be that most braconines that attack deeply concealed, wood-boring hosts are simply not adapted to hit the host's tunnel first and then to use the ovipositor to follow the tunnel to the host, but rather reach their hosts by drilling directly through the substrate to them. If this is generally the case, then the strong, possibly defensive, smell of most braconines (Quicke 1988; Quicke & Wharton in preparation) could be an adaptation to protect them during protracted periods of drilling for hosts, during which time they may be particularly vulnerable to predation.

Interestingly, the Agathidinae and Orgilinae did not appear together in the phylogenetic analyses of Quicke & van Achterberg (1990) and Wharton et al. (1992) though their relationships were rather labile. These two subfamilies have a similar general appearance and perhaps more importantly, have two other putative synapomorphies, a relatively narrow forewing marginal cell with an approximately straight vein 3-SR, and in those species with a complete 2nd submarginal cell, this is small and usually triangular or at least has vein 2-SR very short. The discovery of a new apomorphic character present in both, further suggests the possibility that

they could be sister groups, though the possibility also exists that the ovipositor bending mechanisms possessed by members of the two subfamilies reflect convergence as a result of the similarities in their hosts' biologies. In a preliminary investigation, we have added the presence or absence of an ovipositor boss as an additional character to a data matrix of braconid subfamilies based on that of Quicke & van Achterberg (1990) modified in accordance with the suggestions of Wharton et al. (1992) and of van Achterberg & Quicke (1992). Whereas the Agathidinae and Orgilinae did not appear as sister groups in the most parsimonious trees (length 391), trees with them so arranged were only one step longer than the most parsimonious ones obtained. The absence of this character in the Pselaphaninae might be taken to indicate that they are not the sister group of the Agathidinae (van Achterberg 1985), however, it should be noted that in *Pselaphanus*, the ovipositor is rather robust and is probably unsuited to "steering" and that such a mechanism could have been secondarily lost. In this context, it should also be noted that members of some genera of Agathidinae that have shorter and more robust ovipositors were also found to lack the bosses, and therefore this feature may be readily lost in species whose ovipositors evolve to become less flexible. We therefore conducted a second phylogenetic analysis on the data matrix described above but this time scoring the Pselaphaninae as unknown for the new ovipositor character, thus allowing the possibility of a reversal in that group without adding to tree length. In this case the most parsimonious trees included a subset containing the clade (Orgilinae + (Agathidinae + Pselaphaninae)). We therefore suggest that the newly discovered ovipositor features should be incorporated in future phylogenetic analyses of the Braconidae.

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