

# Comparative morphology of the skeletal parts of the sting apparatus of bees (Hymenoptera: Apoidea)

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Details of the variation in sting morphology for all subfamilies of bees are presented for the first time. A considerable amount of variation, potentially of great utility for phylogenetic studies, has been discovered in every part of this complex structure. Additional probable synapomorphies of bees were found; these include loss of the specialized sensilla-bearing area at the apex of the gonostyli and the reduction and reorientation of the processi mediani at the base of the sting shaft. Synapomorphies for particular subtaxa of bees were found. These include a long, ventral emargination to the second valvifer in Nomiinae and a blister-like protrusion of the lamina spiracularis of the 7th hemitergite in the Megachilinae. Sting reduction and some details of sting morphology would seem to support a relationship between the Stenotritidae and Oxaeinae. Loss of sting function has occurred in four families of bees and repeatedly within the Andrenidae. In some instances loss of function as a sting is associated with increased development of certain structures indicating a change in function for the sting sclerites. It is suggested that all future studies of bee systematics above the species level should include assessment of variation of the sting apparatus and that sting preparations, made and stored in the same manner as preparations of male genitalia, become routine. © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2003, 138, 1–38.

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## INTRODUCTION

The sting of the honey bee was included in the first published use of the microscope; Stelutti's (1625) *Melisso-graphia* and his 'Description of the Bee' published a few years later (Bignami, 2000). Despite this early study, the comparative morphology of the sting apparatus has not received much attention from bee systematists and the utility of the sting sclerites in phylogenetic reconstruction remains largely unexplored. The most extensive representation of variation in bee sting morphology is that of Michener (1944), who included diagrams of the sting apparatus of exemplars from five families. However, in his discussion, treatment of this structure was restricted to statements on the relative length and robustness of the sting in parasitic taxa (p. 216). Hazeltine (1967) illustrated the sting apparatus of ten bee genera from four families and also included a wide range of other Hymenoptera. These two papers are the most detailed

treatments of sting morphology of multiple higher-level bee taxa. Other surveys that have included one or a few bees along with other Hymenoptera are Oeser (1961) and Iuga (1972, 1973). Snodgrass's (1956) study of the honey bee includes the single most detailed account of the sting structure and function for any bee species. Other authors have presented detailed descriptions of the sting apparatus as part of detailed morphological studies of particular bee species or genera: Eickwort (1969) for *Pseudaugochlora graminea* (F.) (Halictidae; Augochlorini), Pesenko (1983) for *Nomioides minutissimus* (Rossi) (Halictidae; Nomioidini), Urban (1967) for *Thygater* (Apidae; Eucerini) and Camargo, Kerr & Lopes (1967) for *Melipona* (Apidae; Meliponini). Roig-Alsina (1989, 1990, 1991) has included diagrams of the sting apparatus in his studies of the cleptoparasitic bee in the tribes Caenoprosopidini, Tetrapedini and Biastini, respectively. Hermann & Mullen (1974) described just the sting apparatus of *Xylocopa virginica* L. (Apidae, Xylocopini) as part of a long series of papers on the sting apparatus of aculeate Hymenoptera with particular emphasis on the Formicidae. In contrast, Poore (1974)

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surveyed just the lancets and gonostyli but did so for a large number of taxa: 37 species of bee from 21 genera in four families along with numerous non-bee aculeates. Weiss (1978) surveyed the stylet and lancets of four species of *Apis*. Sting reduction has been dealt with by various authors, for the Andrenidae by Radovic & Hurd (1980) and Michener (1986), stingless bees by Michener (1990) and the cleptoparasitic Megachilid genus *Dioxys* by Popov (1953). Ultrastructural studies of the sting apparatus of bees have been confined to studies of *Apis* (for example, Shing & Erickson, 1982; Paliwal & Tembhare, 1998). For surveys of the structure and function of the stings of a wider range of aculeate taxa, see Hermann (1984), Hermann & Blum (1981), Maschwitz & Kloft (1971) and Robertson (1968). D'Rozario (1942) studied the development of male and female genitalia in the Hymenoptera, including the honey bee and a colletid. For a description of the actual mechanism of the act of stinging see Snodgrass (1956, pp. 160–164).

Although the potential phylogenetic utility of characters from the sting of aculeate Hymenoptera has been noted (Hermann & Mullen, 1974), Kugler's (1978) study of myrmicine ants is the only phylogenetic analysis based upon sting morphology. In contrast, ovipositor structures are becoming increasingly used in phylogenetic analyses of the Parasitica (e.g. Austin & Field, 1997). Variation in the sting apparatus has been almost completely ignored in studies of bee phylogeny. For example, in Alexander & Michener's (1995) study of short-tongued bees, a data matrix of over 110 characters was constructed of which 47 were from the mouthparts but only one from the sting region (the division of the 7th gastral tergum into two hemitergites – a synapomorphy for bees). It is ironic, but perhaps not surprising, that the most extensive formal use of sting morphology in phylogenetic reconstruction has been in the stingless bees (Michener, 1990). Ruz (1986, 1991) included four characters from the sting in her study of Panurginae, but here too, all four characters were associated with sting reduction and loss of function. The most detailed comparative systematic treatments of the sting apparatus at lower taxonomic levels are by Toro and colleagues who compared structures among genera and subgenera of Xeromelissinae (Aravena & Toro, 1985), among species of *Leioproctus* (Toro & Rojas, 1970; Toro, 1973) and among genera of Panurginae (Ruz, 1986, 1991). In contrast, just the second rami have been used in studies of *Bombus* taxonomy (Richards, 1968).

This paper presents the results of the first complete survey of morphological variation in the sting apparatus of bees, using exemplars from all subfamilies with special emphasis upon those genera used in the recent large-scale phylogenetic analyses of Alexander & Michener (1995). As bees arose from within the sphec-

iform wasps (Brothers, 1975, 1999; Lomholt, 1982; Melo, 1999) some of these were also examined, as was the Pompilid *Anoplius*, the same genus as used by Alexander & Michener (1995) as their sole non-apoid exemplar. Treatment of the wasps is largely restricted to major differences between them and bees. For a complete list of taxa, see Table 1.

I have two main purposes. First, I wish to bring the rich variation in structure of the sting apparatus of bees to the attention of bee systematists and to students of other groups of Hymenoptera. Secondly, I wish to provide detailed descriptions and diagrams/microphotographs of the structures involved. Detailed analyses of morphological changes associated with sting reduction or accompanying the evolution of cleptoparasitism will be dealt with elsewhere. Herein, references to such aspects are restricted to those associated with the particular exemplars used.

## TERMINOLOGY

### MORPHOLOGICAL

'there is still much unavoidable discrepancy in the use and application of anatomical names in entomology. The trouble, in large measure, can be blamed on the insects themselves', Snodgrass (1935).

There has been considerable variation in the terminology used for different parts of the ovipositor of insects, especially for the Hymenoptera because of its elaboration into a saw-like structure in the Symphyta, a drill in many of the Parasitica and as a sting in the Aculeata. Oeser (1961) tabulated the nomenclature used for each major part of the hymenopteran ovipositor for every paper on the subject from Westwood (1840) through to Hennig (1959); his table runs to 13 pages. Similarly, Smith (1970) listed synonymies and authorships for all terms associated with the hymenopterous ovipositor and added many new terms; his glossary runs to almost six pages. Tuxen (1956) provides a complete list of terms associated with the genitalia of all insects and entognathous hexapods.

Students of different taxonomic groups commonly use different terms for homologous structures. In this paper, I follow the standard terminology as used by researchers into the systematics and anatomy of bees (see Michener, 2000). A brief outline of the terms for major components of the sting apparatus is as follows. Each half of the divided terga of the 7th and 8th gastral segments is referred to as the 7th or 8th hemitergite. These have often been termed the spiracle and quadrate plates, respectively (Sollman, 1863; Beyer, 1891; Snodgrass 1956). The first valvifer, which originated from the appendage of the 7th gastral segment, has commonly been referred to as the triangular plate

**Table 1.** List and classification of taxa used in this study

Family	Subfamily	Primary exemplars	Additional study taxa
Stenotritidae		<i>Stenotritus</i> sp. <i>Ctenocolletes smaragdinus</i> (Smith)*	
Colletidae	Colletinae	<i>Colletes halophilus</i> Verhoeff	<i>Calomelitta</i> sp. <i>Eulonchopria</i> sp. <i>Leioproctus atacama</i> Toro & Rojas <i>Lonchopria zonalis</i> Reed <i>Mourecotelles mixta</i> Toro & Cabezas <i>Scrapper nitidus</i> (Friese)
	Xeromelissinae	<i>Chilicola polita</i> Michener	
	Hylaeinae	<i>Hylaeus pectoralis</i> Forster	<i>Amphylaeus</i> sp. <i>Hyleoides</i> sp. <i>Meroglossa</i> sp.
	Diphaglossinae	<i>Crawfordapis luctuosa</i> (Smith)	<i>Cadeguala occidentalis</i> (Haliday) <i>Caupolicana gayi</i> Spinola <i>Diphaglossa sayi</i> Spinola <i>Mydrosoma serratum</i> (Friese)
Andrenidae	Euryglossinae	<i>Euryglossa</i> ( <i>Euryglossa</i> ) sp.	
	Alocandrenidae	<i>Alocandrena porteri</i> Michener*	
	Andreninae	<i>Andrena nitida</i> (Moller)	<i>Ancylandrena atoposoma</i> Cockerell <i>Euherbstia excellens</i> Friese <i>Megandrena mentzeliae</i> (Cockerell)* <i>Orphana inquirenda</i> Vachal* <i>Macrotera texana</i> (Cresson)* <i>P. (Mesoxaea) rufescens</i> Hurd & Linsley* <i>P. (Notoxaea) ferruginea</i> (Friese)* <i>Oxaea flavescens</i> Klug*
	Panurginae	<i>Protandrena</i> sp.	
	Oxaeinae	<i>Protoxaea</i> ( <i>P. gloriosa</i> ) Fox*	
Halictidae	Rophitinae	<i>Systropha planidens</i> (Girault)	
	Nomiinae	<i>Dieunomia heteropoda</i> (Say)	<i>Nomia</i> ( <i>N. melanderi</i> ) Cockerell <i>N. (Crocisaspidia)</i> sp. <i>N. (Hoplonomia)</i> sp. <i>Pseudapis</i> sp.
Melittidae	Halictinae	<i>Corynura chloris</i> (Spinola)	<i>Halictus ligatus</i> Say
	Dasypodainae	<i>Dasypoda altercator</i> (Harris)	<i>Hesperapis laticeps</i> Crawford <i>Capicola rufiventris</i> (Friese) <i>Haplomelitta ogilvei</i> (Cockerell)
	Meganomiinae	<i>Meganomia gigas</i> Michener	
	Melittinae	<i>Macropis nuda</i> Provancher <i>Melitta tricincta</i> Kirby	<i>Redivivoides simulans</i> Michener
Megachilidae	Fideliinae	<i>Fidelia</i> ( <i>F. villosa</i> ) Brauns <i>Pararophites orobinus</i> (Morawitz)	<i>F. (Parafidelia) pallidula</i> <i>Neofidelia profuga</i> Moure & Michener
	Megachilinae	<i>Lithurgus</i> sp. <i>Megachile centuncularis</i> (L.) <i>Trachusa perditia</i> Cockerell	<i>Microthurge pygmaeus</i> (Friese) <i>Trichothurgus</i> sp. <i>Ochreriades fasciatus</i> (Friese) <i>Afroheriades dolicocephalus</i> (Friese) <i>Coelioxys rufescens</i> (L.) <i>Hoplitis claviventris</i> (Thomson) <i>Megachile disjunctum</i> (F.) <i>Osmia leaiana</i> (Kirby) <i>Protosmia ribifloris</i> (Cockerell) <i>Manuelia gayi</i> (Spinola)
Apidae	Xylocopinae	<i>Xylocopa tabaniformis</i> Smith	
	Nomadinae	<i>Epeolus</i> sp.† <i>Nomada flava</i> Panzer†	
	Apinae	<i>Eucera longicornis</i> (L.) <i>Leiopodus abnormis</i> Jorgensen†	<i>Exomalopsis</i> sp. <i>Amegilla subcaerulea</i> (Lep.)  <i>Coelioxoides waltheriae</i> Ducke† <i>Ctenoplectra vagans</i> Cockerell <i>Osiris mourei</i> †

Table 1. *Continued*

Family	Subfamily	Primary exemplars	Additional study taxa
Apoid Wasps			
Heterogynaeidae		<i>Heterogyna</i> sp.	
Ampulicidae		<i>Dolichurus greenei</i> Rohwer	
Sphecidae		<i>Sphex latreillei</i> Lep.	
Crabronidae	Astatinae	<i>Tachytes fulviventris</i> Cresson	<i>Pulverro columbianus</i> (Kohl)
	Philanthinae	<i>Philanthus triangulum</i> (F.)	
	Mellinae	<i>Mellinus arvensis</i> (L.)	
	Pemphredoninae	<i>Pemphredon lugubris</i> (F.)	<i>Stigmaeus solskyi</i> Morawitz <i>Passaloecus corniger</i> Shuckard <i>P. monilicornis</i> Dahlbom <i>Psen unicolor</i> (Panzer) <i>Diodontus luperus</i> Shuckard <i>Psenulus pallipes</i> (Panzer)
Vespoidea			
Pompilidae		<i>Anoplius bengtssoni</i> (Regan)	

\*Taxa with marked sting reduction.

†Cleptoparasitic taxa.

(Cameron, 1882; Snodgrass, 1956) or gonoplac (Scudder, 1961; Kristensen, 1991). Basally, it gives rise to a long thin process called the first valvula. The basal part of the first valvula is the first ramus and the more apical part the lancet, which itself gives rise to the valvilli (lancet valves). The appendage-derived structures of the eighth gastral segment are called the second valvifers. These are termed oblong plates by some researchers (Sollman, 1863; Snodgrass, 1956). Basally, the second valvifers give rise to the second valvulae. Initially these are narrow, separated and form the second rami, but apically they are fused to form the sting shaft. Apically, the second valvifers give rise to the gonostyli, often incorrectly called the third valvulae or sting sheaths; they are not homologous with the first and second valvulae and often do not function as sheaths (Scudder, 1961; Michener, 2000). Table 2 presents the terms used in this paper along with the synonyms that are often found in the literature.

Wherever possible, structures derived from terga are treated as if they were horizontal plates. As is the case with the external metasomal segments, the apodeme is taken to arise from the anterior margin of the plate. Posterior and lateral margins are identified using the apodeme as a landmark for the anterior margin. Because terga 7 and 8 have become divided longitudinally, each half also has a medial margin. In the evolution of the ovipositor and then the sting, considerable modification of the original structures has taken place such that morphologically anterior, posterior, lateral and medial margins commonly have completely different orientations. Nonetheless, wherever possible, the original morphological orientations are

used for two reasons. First, some structures seem capable of considerable movement thereby rendering superficial use of terms of orientation confusing. Second, considerable change in shape has occurred in some sclerites such that in some taxa different parts of the same structure may be in very different orientations with respect to one another. In some instances, use of morphologically accurate terms of orientation leads to statements which are almost impossible to follow with respect to the actual location of structures within the insect. This is particularly the case with the second valvifer. The more informal terms upper, basal, inner, etc. are used in such instances, based upon the orientation of the structures within the insect at rest.

#### SYSTEMATIC

Traditionally, the bees and those wasps most closely related to them have been given equal taxonomic rank: they have been known, at least informally (Brothers, 1975; Finnamore & Michener, 1993), as the Apiformes (bees) and the Spheciformes (the Spheciform wasps = Sphecidae *sensu* Bohart & Menke, 1976). It is now well established that bees render the spheciform wasps paraphyletic (Lomholt, 1982; Alexander, 1992; Melo, 1999) making the previous classification problematic. It is also clear (Melo, 1999) that two or three clades of apoid diverged before the dichotomous branch between the bees and the remaining apoid wasps. These are the Heterogynaeidae, Ampulicidae and Sphecidae (*s.s.*). Melo (1999) united the remaining 'Spheciform' wasps as a single family, the Crabronidae, which his analysis

**Table 2.** Major synonyms for morphological terms used with respect to the sting apparatus

Term used herein	Most commonly used synonyms
7th hemitergite (gastral or metasomal)	Spiracle plate 8th hemitergite (abdominal)
8th hemitergite (gastral or metasomal)	Quadrate plate 9th hemitergite (abdominal)
First valvifer	Triangular plate Gonocoxite VIII Gonocoxite 1 (genital) Gonangulum
First ramus of first valvula	Gonapophysis VIII Gonapophysis 1 (genital)
Second valvifer	Oblong plate Gonocoxite IX Gonocoxite 1 (genital)
Gonostylus	Sting sheath Ovipositor sheath 3rd valvula Gonoplac
Second ramus of second valvula	Gonapophysis IX Gonapophysis 2 (genital)
Sting shaft	Fused gonapophyses 1 Fused gonapophyses 2 (genital) Fused second valvulae

suggests is the sister group to the bees. He similarly treated the bees as comprising a single family. This latter decision seems to obscure much of the large amount of variation and diversity found among bees (Michener, 2000). Consequently, in this work, I follow Michener (2000) in treating bees as belonging to seven different families; the Colletidae, Stenotritidae, Andrenidae (including the Oxaeinae), Halictidae, Melittidae, Megachilidae and Apidae (including the Anthophorinae). Whenever the apoid wasps and *Anoplius* are being referred to together, I simply refer to them as wasps and whenever the non-bee apoids are referred to as a group I use the term apoid wasps. Michener's (2000) classification of the bees below the family level is also used throughout.

## METHODS

The sting apparatus was removed from bees that had been left in a relaxing chamber for at least 24 h. They were excised using fine forceps and/or entomological pins, and placed in a 10% solution of potassium hydroxide at room temperature for between 4 and 8 h. Large pieces of soft tissue were removed using pins and fine forceps during this time. Clearing was followed by neutralization in 5% acetic acid and storage

in glycerine. Thus, the female terminalia were treated in more or less exactly the same way as is usually the case for male genitalia (e.g. McGinley, 1986). Multiple preparations of some common North American genera were mounted on microscope slides with permount to assess intraspecific variation. At least two preparations were made of some genera which possessed unusual features, such as *Crawfordapis*, *Orphana*, *Macrotera*, *Dasyroda*, *Melitta* and *Macropis*. Intraspecific variation was minimal and is not dealt with further.

Most microphotographs were taken using a Leica M5 microscope fitted with a Wild MPS52 camera and digital images were obtained with a Leica M12.5 with a Photometrix coolsnap colour digital camera. Smaller sting parts, such as most first valvifers, were photographed using the MPS52 attached to a Leitz Dialux 20EV compound microscope. The images were processed using Photoshop, particularly the 'sharpen more' algorithm. Temporary mounts were made of comparatively flat structures (such as the hemitergites) using microscope slides, cover slips and a small amount of glycerine. Some structures could not be flattened appropriately without damage and, in these instances, glycerine-filled depressions in ceramic tiles were used to house material for photography.

Exemplar taxa (Table 1) were chosen from all bee families and subfamilies as defined by Michener (2000). Wherever possible, the same species, or at least genera, were used as those studied by Alexander & Michener (1995). In addition to these 27 species, representatives of many other bee genera, ten genera of apoid wasps and the pompilid genus *Anoplius* were also studied. Only the 27 bee, six primary apoid wasp exemplars and the single vespoid were exhaustively studied for variation in all parts of the sting apparatus. Treatment of the additional bee taxa is largely restricted to notably unusual features, extreme variants or character states found in the primary exemplars which seemed to have potential as synapomorphies for a higher-level taxonomic group. Special emphasis is placed upon taxa of uncertain affinities but whose placement is likely to be important for higher-level bee phylogeny. Thus, the Stenotritidae, Oxaeinae, and Melittidae (Michener, 2000; the latter including the Meganomiidae, Dasypodaidae AND Melittidae of Alexander & Michener, 1995) are treated in a little more detail than well known monophyletic units such as the Megachilidae and Apidae (*sensu* Roig-Alsina & Michener, 1993). The wasps were included for comparative purposes and to see whether additional possible synapomorphies for bees could be discovered. The Pemphredoninae were treated more extensively than were the remaining apoid wasp taxa because preliminary observations suggested some interesting similarities between them and at least some of the bee exemplars, in particular some presumably convergent features of the 7th hemitergites.

## BASIC DESCRIPTION OF THE STING APPARATUS

### OVERALL STRUCTURE

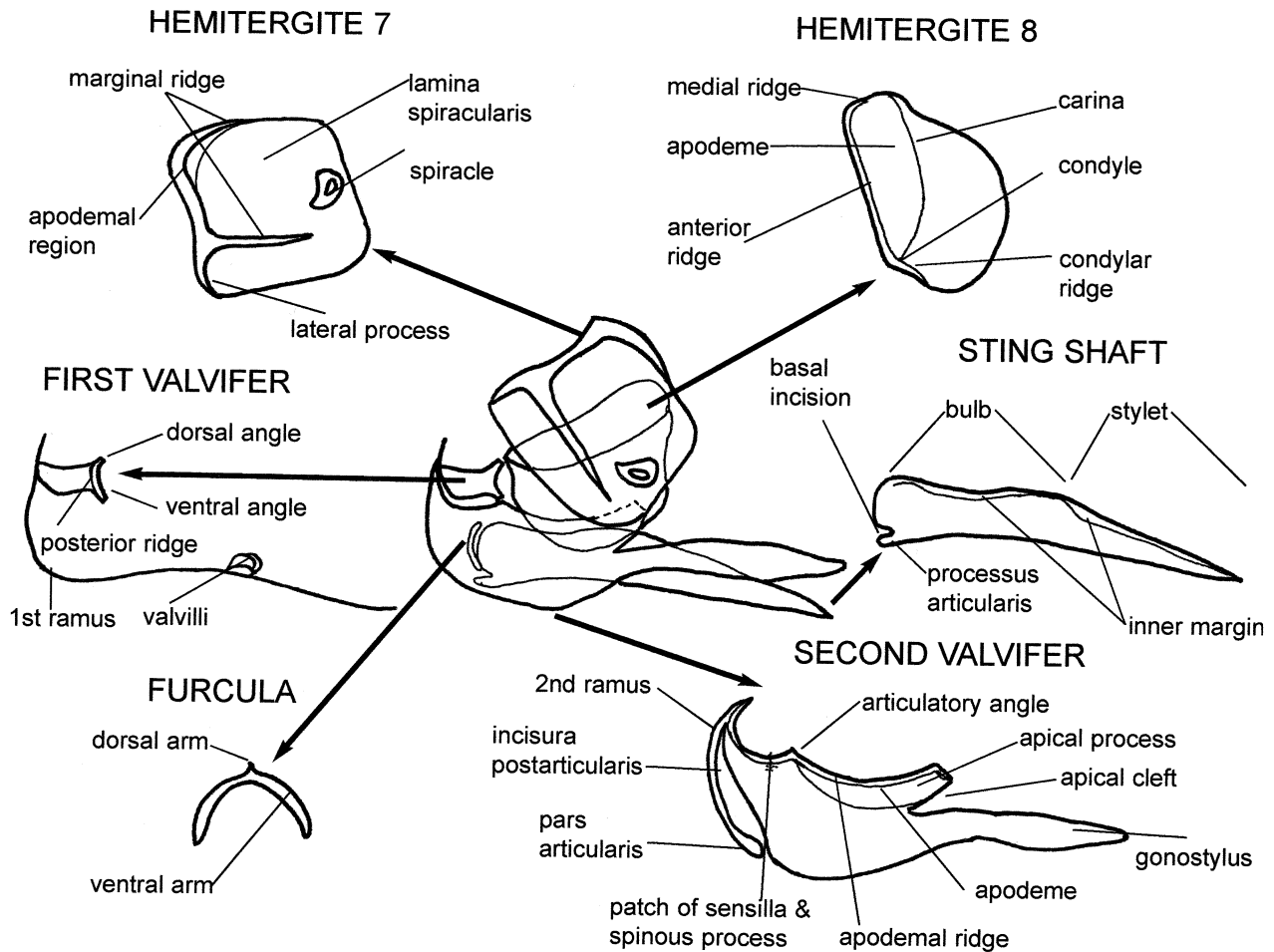
The sting apparatus of bees and aculeate wasps is housed in the sting chamber formed by the 6th gastral segment (Snodgrass, 1956). In comparison to the less-derived condition found in Symphyta and many non-hymenopterous insects, the 7th and 8th gastral segments have become internalized within the sting chamber (Snodgrass, 1956; Oeser, 1961). The terga of the 7th and 8th segments remain, both divided longitudinally into hemitergites, but the sterna have been lost (Snodgrass, 1956; Smith, 1970). The 9th gastral segment is so reduced and desclerotized as to be difficult to discern, at least in most bees (Michener, 1944; Snodgrass, 1956) and is not treated here. The remaining sclerotized parts of the sting apparatus are derived from gonocoxal appendages (Smith, 1970).

Figure 1 shows the relative position of the various parts in diagrammatic form along with their morphologically correct orientations where it is possible to

deduce this. Figure 1 also shows the terms used for the various parts of each structure in the following account. The outermost parts are the 7th hemitergites. Although in most wasps these structures are joined by a sclerotized bridge, in all bees and a few Apoid wasps the hemiterga are separate, joined only by membrane (Hazeltine, 1967; Melo, 1999). The 8th hemitergites are more mesad and slightly more ventrally positioned with respect to the 7th hemitergites. Each bears a large apodeme which is orientated dorsal to the tergite in the insect at rest, although morphologically it is anterior. Mesad to the 8th hemitergites, the second valvifers curve ventro-medially towards the sting shaft. These are thought to have been derived from the subcoxa, coxa and coxosternite of the 8th gastral segment (Smith, 1970). In a posterior direction, each second valvifer gives rise to a long, somewhat cylindrical structure which, by melittologists, has usually been called the gonostylus. This actually arises from the morphologically lateral surface (Smith, 1970). From the basal portion of each of the second valvifers a long, thin process curves downwards and then posteriorly eventually forming an articulation with a process arising from the antero-ventral margin of the sting shaft. This is the second ramus, the basal part of the second valvula. Apically, the second valvulae are fused to form the sting shaft. The first valvifer is a comparatively small but heavily sclerotized structure. It has two posterior angles, the dorsal one articulates with the 8th hemitergite and the ventral one with the second valvifer. Anteriorly, the first valvifer gives rise to a long thin sclerotized structure which basally forms the first ramus, which is narrow, like the second ramus, with which it forms a sliding interlocking device called the olistheter (Smith, 1970). Posteriorly, the first rami extend as the lancets which form the ventral portion of the sting itself and bear two chitinous flaps arising from a dorsal swelling. These projections have been termed valves (Snodgrass, 1956) although Quicke, Fitton & Ingram (1992) comment that they do not always function as such in those taxa that possess them and recommend use of the term valvilli. The anterior portion of the sting shaft is swollen dorsally and laterally to form the sting bulb which tapers to a stylet apically. A Y- or wishbone-shaped furcula articulates with the anterior surface of the sting shaft and projects dorsally and/or posteriorly dorsal to the base of the sting shaft bulb. It appears to be derived from a detached anterior portion of the sting shaft (Smith, 1970; Hermann & Chao, 1983).

### VARIATION IN OVERALL APPEARANCE

Most bees conform to the general pattern outlined above with the relative positions of the various parts



**Figure 1.** Lateral view of the sting apparatus of a generalized bee, *Andrena pubescens* as found at rest, with each individual structure shown separately in the position interpreted to represent its morphologically correct orientation where this is possible. Anterior to the left. For the hemiterga, the lateral margins are towards the bottom of the figure, medial margins towards the top. This figure is generally representative of the structures found in all bees with the exception of the unusually short dorsal arm to the furcula in this genus.

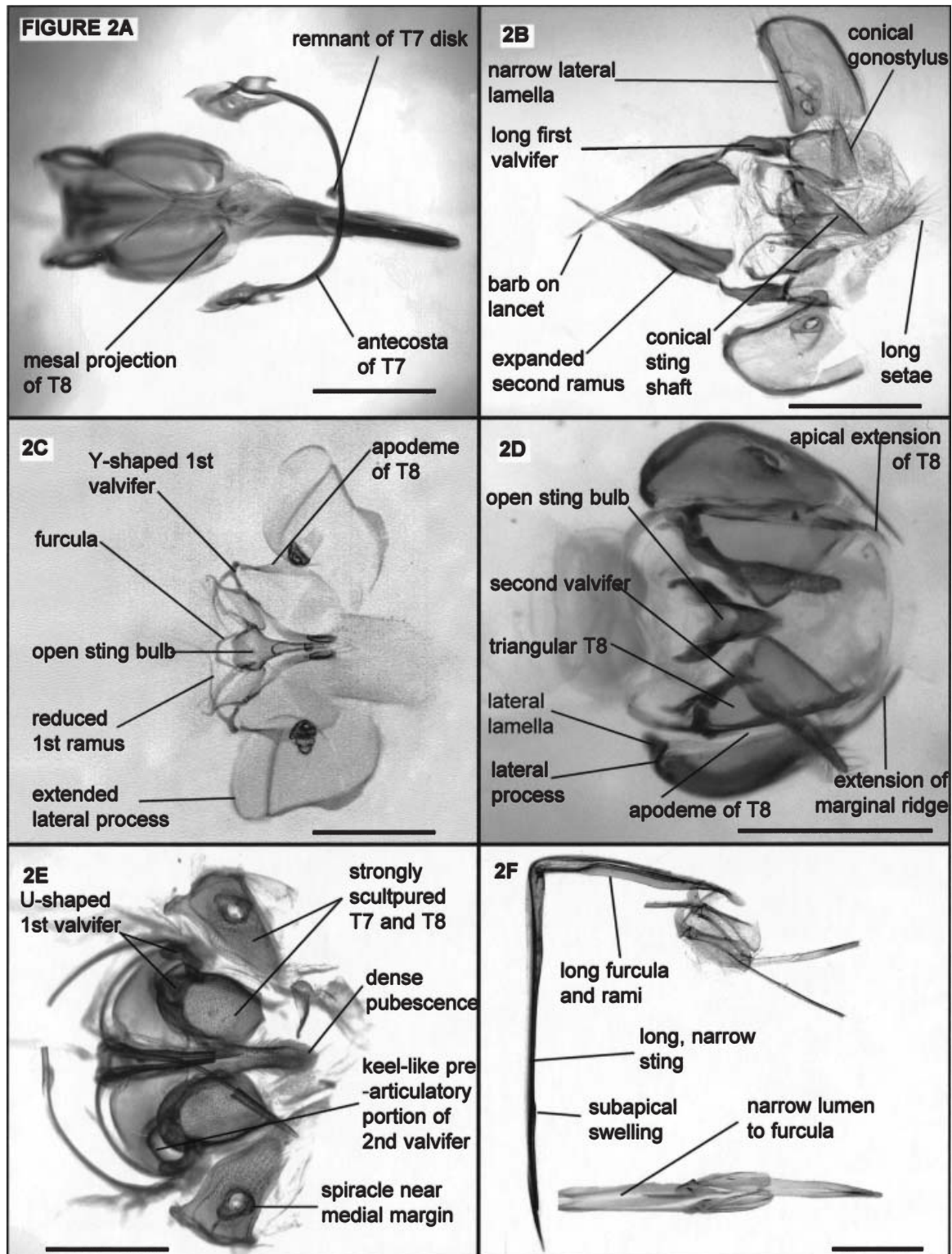
more or less similar in all taxa. However, several large scale variants have been noticed which deserve mention at this point.

Sting reduction results in considerable evolutionary modification of all parts of the sting (Fig. 2B–D). It has occurred independently in numerous bee lineages. This will be dealt with in detail elsewhere but some aspects are noted in the present account, separately for each structure, because some important exemplars are members of higher level taxonomic groupings all (e.g. Stenotritidae), or many (e.g. Andrenidae), of which have reduced stings.

In *Trachusa* the 7th and 8th hemitergites and second valvifers are orientated more horizontally than in other bees and this imparts an unusually flattened appearance to the whole sting apparatus (Fig. 2E). This was noticed for another Anthidiine, *Dianthidium*

*sayi*, by Michener (1944: fig. 233). At the opposite extreme is the situation found among the cleptoparasitic Apidae studied here, and also *Coelioxys*, in which the 7th and 8th hemitergites and second valvifers are orientated much more vertically than in other bees, giving the whole sting apparatus a very narrow aspect (Fig. 2F). All other bees studied are intermediate in the orientation of the plates such that in dorsal view the sting apparatus appears somewhat open, but certainly not as flat as in *Trachusa*.

Another feature common to the cleptoparasitic Apidae is a comparative lengthening of the furcula and first and second rami (Fig. 2F). This enables the sting shaft to be held at some distance from the sting plates and permits considerable extension of the sting outside of the gaster. This is most marked in *Coelioxoides* (see Roig-Alsina, 1990; his fig. 13a) and *Osiris*



**Figure 2.** Variation in overall appearance of the sting apparatus in bees and apoid wasps. Anterior to the left, scale bar = 1 mm. (A) *Tachytes*, dorsal view, (B) *Orphana*, ventral view of partially flattened apparatus with second rami pushed out of position towards the anterior. (C) *Stenotritus*, ventral view of partially flattened apparatus. (D) *Ctenocolletes*, ventral view. (E) *Trachusa*, ventral view of slightly flattened apparatus. (F) *Osiris*, lateral view with inset showing dorsal view of all but the sting shaft; 7th hemiterga omitted in both parts of this figure; the sting has been pulled down from the rest of the apparatus, and so for the sting shaft the anterior end is towards the top of the figure.



(Fig. 2F); many museum specimens of the latter genus have the entire sting shaft exerted from the abdomen and reflexed over the gastral dorsum. The 7th and 8th hemitergites and second valvifers seem small in comparison to the other parts of the sting in these cleptoparasitic taxa (Fig. 2F).

The degree of sclerotization of the sting sclerites is variable. In bees with sting reduction some parts of the sting often become desclerotized, particularly the lancets (Figs 2C, 8G). However, the reduced parts that remain are often more heavily or uniformly sclerotized than in related taxa without reduced stings. *Ctenocolletes* in particular has a well-sclerotized apparatus in comparison even to its closest relative *Stenotritus* (compare Fig. 2C with 2D), although in both the apparatuses are non-functional (at least as stings). The overall structure of the sting apparatus of *Ctenocolletes* is sufficiently unusual for several of its parts to be treated independently of the variation found among the rest of the bees in the accounts that follow. Houston (pers. comm.) states that the sting apparatus of four other species of *Ctenocolletes* are very similar to the exemplar used here.

## DESCRIPTIONS OF THE SEPARATE PARTS

Some parts of the sting apparatus show markedly more variation than do others. The degree of variation does not necessarily correlate with the complexity of the structure, as the amount of descriptive detail provided below is most extensive for the 7th hemitergites which are relatively simple structures. The more complex second valvifers (with associated rami and gonostyli) receive a similar amount of attention whereas the remaining sclerites require less detailed treatment. However, considering its structural simplicity, the furcula exhibits a remarkable array of variation.

### 7TH HEMITERGITE

#### *Basic structure and homology*

Each of the 7th hemitergites (Figs 1–5) is composed of a lamina spiracularis largely surrounded by a heavily sclerotized marginal ridge which bears a narrow process and lamella laterally. Within the lamina spiracularis there is a spiracle and associated atrium, apodemes and trachea.

In *Anoplius* and the non-pemphredonine apoid wasps examined, there is a strongly sclerotized bridge which unites the two halves of the 7th tergum (Fig. 2A, 8A) and which precludes independent movement of the two halves. This bridge, which is approximately at right angles to the long axis of the tergum, bears a strong internal ridge which is presumably homologous to the antecosta of the preceding segments. Although this is morphologically anterior, the

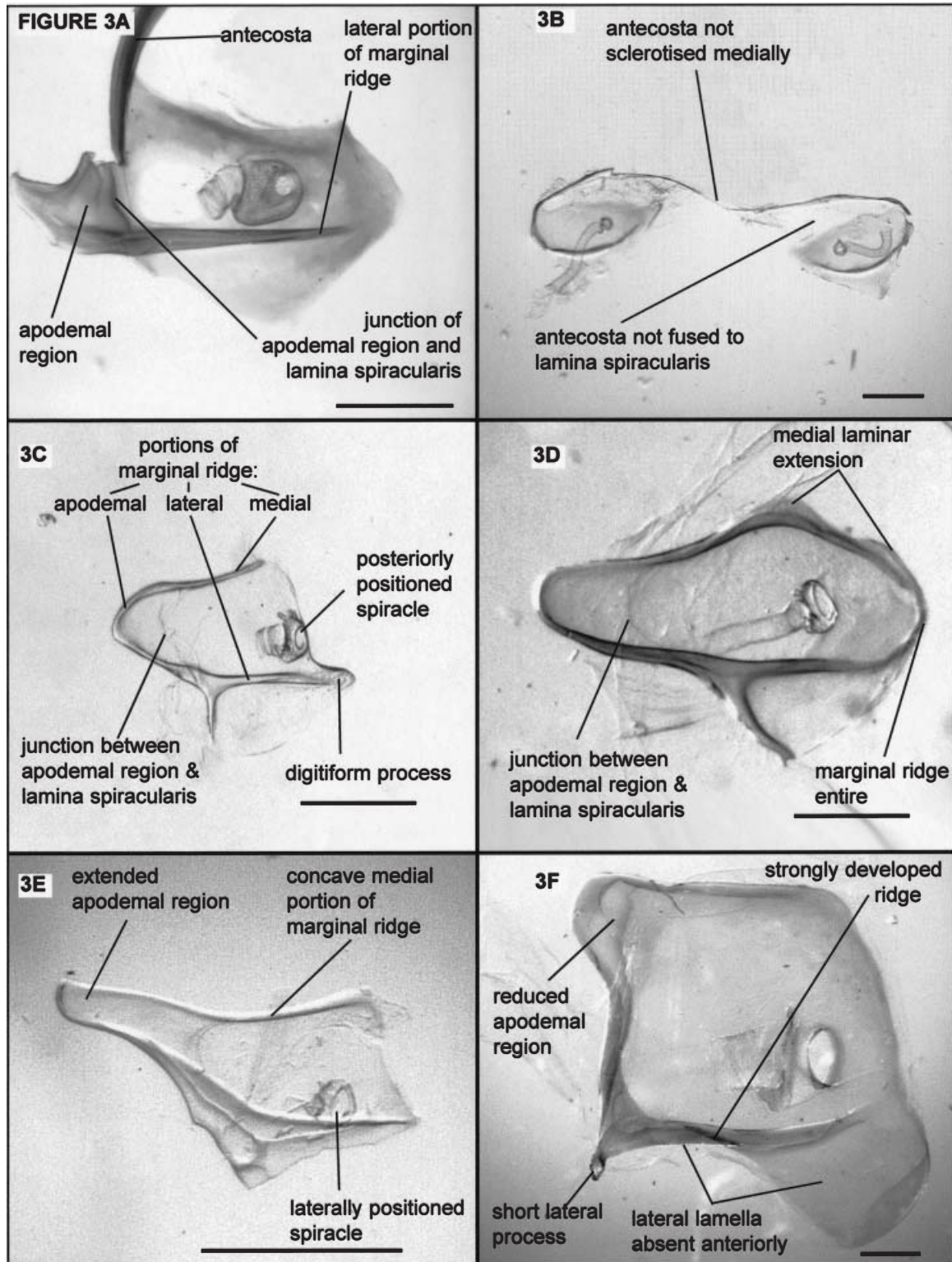
entire 7th tergum of the wasps is rotated posteriorly such that the antecosta is postero-dorsal with respect to the remaining sclerites of the sting apparatus. Some remnants of the disc of the plate can be found as a small medial triangular sclerotization on the posterior margin of the antecosta in *Tachytes* (Fig. 2A) and *Philanthus*.

The middle portion of the antecosta is divided medially (at least narrowly) in the pemphredonines examined (Fig. 3B), except *Psenulus* and *Diodontus* in which it is narrowed but not completely divided. The Astatine *Pulverro* has completely and widely separated hemiterga as in the bees (Melo, 1999; pers. observ.). In the pemphredonines, the free portion of this antecostal ridge is rotated posteriorly to an acute angle – around 20° – to the medial margin of the lamina spiracularis which, in these wasps, is otherwise lacking any thickened medial margin (Fig. 3B). In most bees, if anything remains of the antecosta, it is fused to the medial margin of the lamina spiracularis (Figs 2B, 3C–F, 4A,D,E, 5A–F) and forms the medial portion of the marginal ridge.

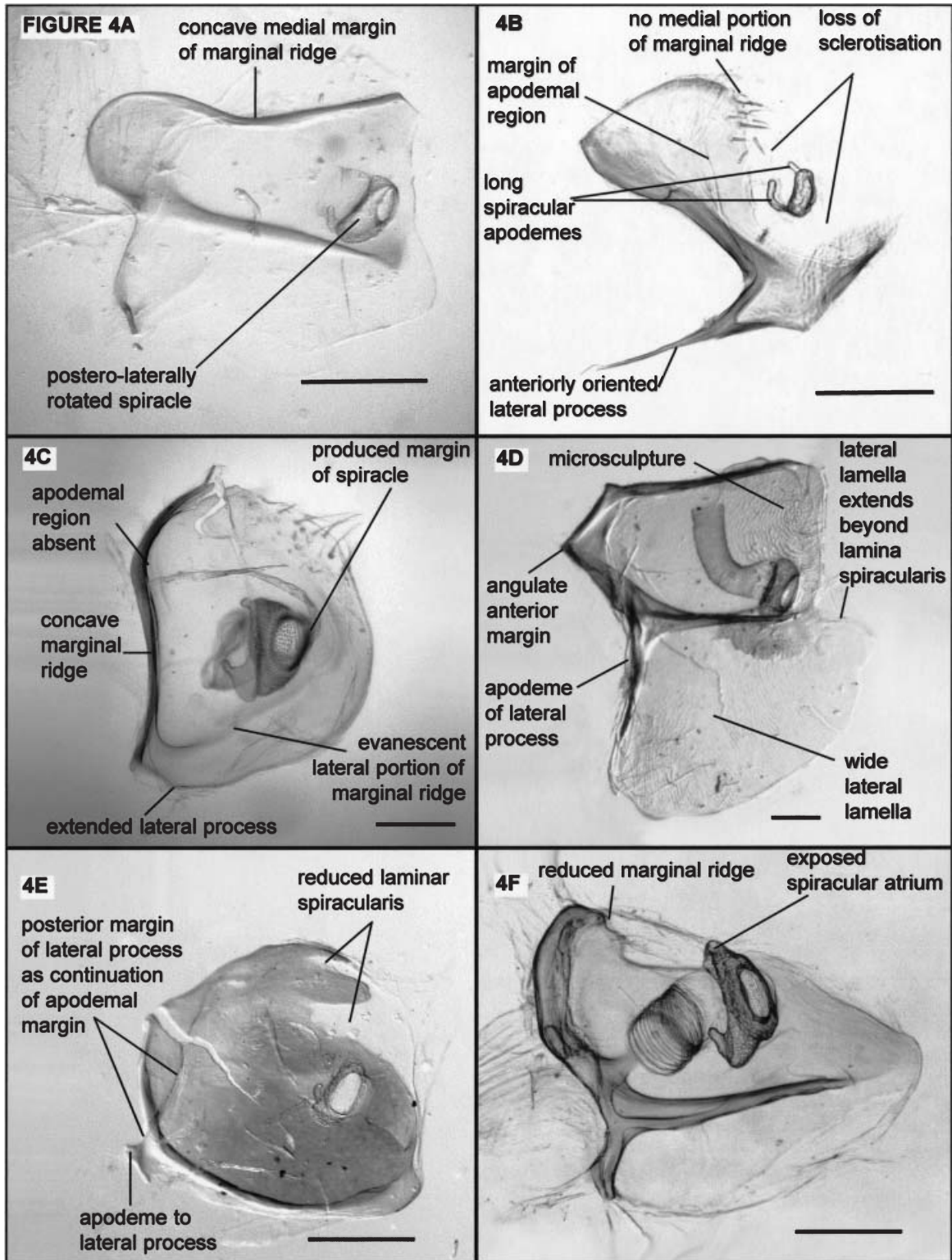
Gastral terga 2–6 each have an anterior apodeme on either side. On the 7th tergum of *Tachytes* this can be seen as a triangular, anteriorly directed projection originating from the antero-lateral margin (Fig. 3A). In *Sphex* the apodeme is shorter and deflected medially. In most bees, and some apoid wasps, the apodemal region seems to be detectable only by a slight anterior thickening of the lamina spiracularis (Figs 3C–E, 4B). The apodemal region is more obvious in some Apidae (Fig. 5C–E) in which a distinct ridge separates it from the lamina spiracularis. Conversely, in some bees the apodemal region is very short and indistinguishable from the marginal ridge (Fig. 4C,F).

The 7th hemitergite is largely surrounded by a marginal ridge which can be divided into lateral, apodemal and medial portions (Fig. 3C). A lateral process extends from the lateral portion of the marginal ridge. This process usually appears as an extension of the posterior margin of the apodemal region, i.e. it arises where the junction between the lamina spiracularis and apodemal region meets the marginal ridge laterally (Figs 4E, 5A,F, but see 5E). In some taxa the junction of lamina spiracularis and apodemal ridge is continuous with the anterior edge of the lateral process (Figs 4E, 5A), in others it is continuous with the posterior margins of this process (Fig. 5F). The elongate lamella subtended by the lateral process and lateral portion of the marginal ridge is termed the lateral lamella.

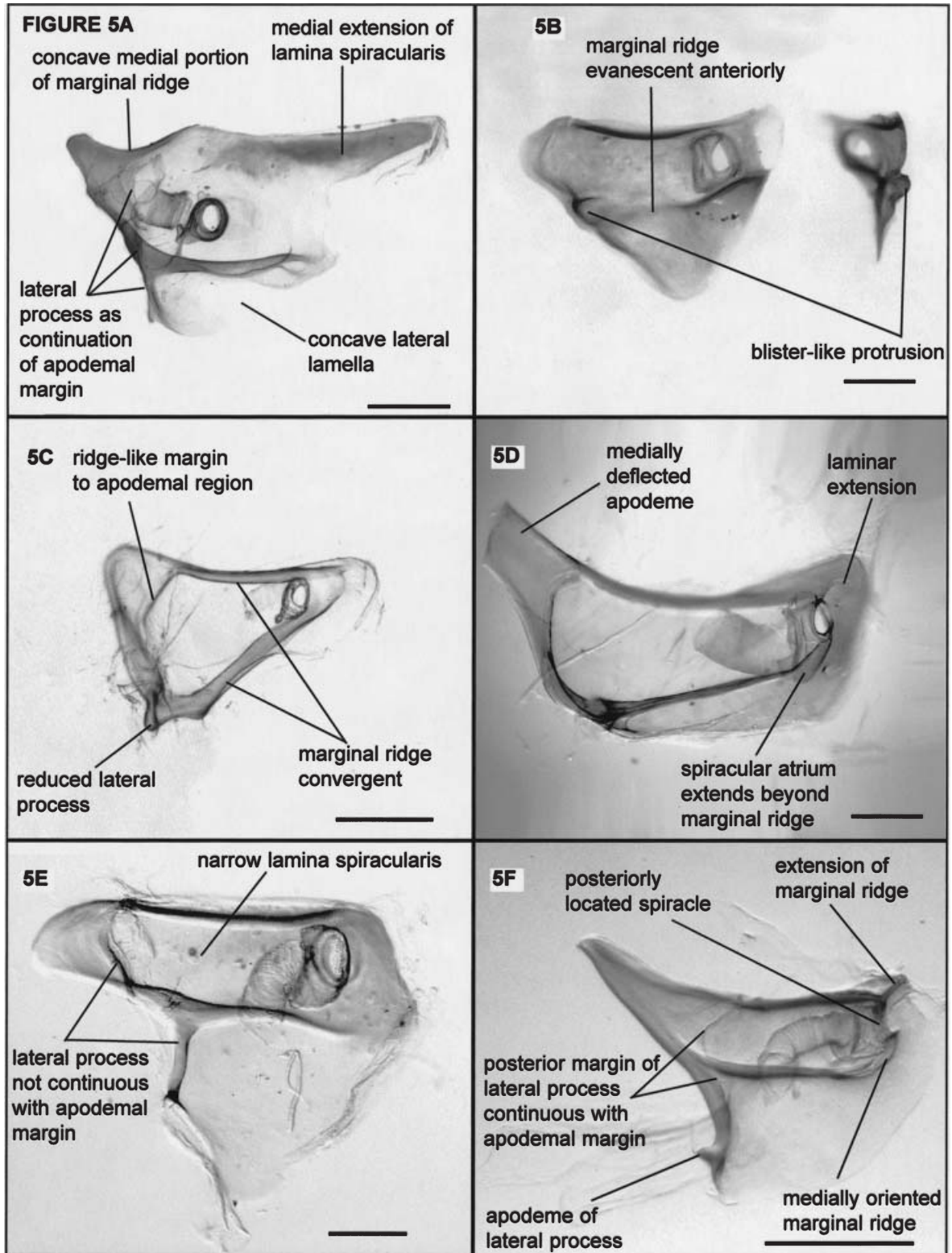
As one of its synonyms (spiracle plate) implies, the 7th hemitergite bears a spiracle and accompanying spiracular atrium, apodemes to the spiracular atrium and trachea. These are the only large components of the gas exchange system found in the sting apparatus.



**Figure 3.** Variation in structure of 7th hemitergites of crabronid wasps and bees of the family Colletidae, views of morphologically dorsal surface with anterior to the left. In this figure and Figs 4 and 5, the tubular structure arising from the spiracular opening is the trachea of the 7th gastral segment. Scale bar = 0.25 mm. (A) *Tachytes*. (B) *Pemphredon*, hemitergites of both sides showing incomplete sclerotized bridge between them. (C) *Euryglossa*. (D) *Hylaeus*. (E) *Chilicola*. (F) *Crawfordapis*.



**Figure 4.** Hemitergites of various short-tongued bees other than Colletidae, views of morphologically dorsal surface anterior to the left. Scale bar = 0.25 mm. (A) *Protandrena*. (B) *Macrotera*. (C) *Protoxaea*. (D) *Dieunomia*. (E) *Dasyroda*. (F) *Meganomia*.



**Figure 5.** Variation in hemitergites of various long-tongued bees, views of morphologically dorsal surface anterior to the left unless stated otherwise. Scale bar = 0.25 mm. (A) *Fidelia*. (B) *Megachile*, dorsal view on left, posterior view on right to show blister-like protrusion in profile. (C) *Epeolus*. (D) *Xylocopa*. (E) *Eucera*. (F) *Leiopodus*.

The two apodemes arise from the anterior margin of the spiracular atrium and are dissimilar in size, the lateral one being the larger of the two.

#### Variation

The overall shape of the 7th hemiterga varies considerably. In most taxa the marginal ridge forms a V or U shape (Figs 2B, 3C, 4A), with the opening orientated posteriorly and the apodemal region at the fulcrum. The apodemal region may be greatly produced anteriorly as in *Chilicola* and *Leiopodus* (Figs 3E, 5F), giving the hemitergite an elongate V-shape. The apodemal region is deflected medially in *Xylocopa* (Fig. 5D), in which it appears almost like the handle of a revolver. In *Crawfordapis* a distinct apodemal region is separate from the marginal ridge for only the most medial third of the hemitergite (Fig. 3F). Other Diphaglossines are similar in this respect, although the apodemal region is more strongly produced in *Mydrosoma*. In all other bees with a well-developed antecostal region, it extends for more or less the entire breadth of the hemitergite anteriorly and it is this region which often gives the rounded fulcrum to the U, or angle to the V-shaped hemitergite (Figs 3C,D, 4A, 5E,F). In *Dieunomia* (Fig. 4D) the apodemal region is angularly produced anteriorly making it V-shaped, although the medial and lateral portions of the marginal ridge are quite straight and parallel to one another.

Other than the U- and V-shaped plates, the overall form of the hemitergite may be circular, triangular, oval, semicircular, rectangular or square. In *Dasypoda* (Fig. 4E) both medial and lateral portions of the marginal ridge are convex and, although the two do not come close to meeting posteriorly, combined with the partly convex posterior margin of the lamina spiracularis, they give the plate an almost circular aspect. In *Epeolus*, *Xylocopa* (Fig. 5C,D) and *Nomada* the medial and lateral portions of the marginal ridge converge posteriorly, and apically almost surround the comparatively posteriorly located spiracle. In the two cleptoparasitic genera they converge sufficiently uniformly and markedly from a broad apodemal region to make the plate approximately triangular (Fig. 5C). In *Colletes* (but not the other Colletinae) and all Hylaeinae the hemitergites are long and oval in shape and the marginal ridge is continuous posteriorly such that the lamina spiracularis is completely encircled (Fig. 3D). In Oxaeinae, the apodemal region is slightly concave (it is straight in the subgenus *Notoxaea*), the medial and lateral portions of the marginal ridge are very short, and the lamina spiracularis curves mesally on both sides such that the whole sclerite appears semicircular or D-shaped (Fig. 4C). In *Megachile*, *Eucera* and *Leiopodus* the area subtended by the marginal ridge is unusually narrow, making the

hemitergite more oblong in shape and much longer than wide (Fig. 5B,E,F). Lastly, the hemitergites may be square as a result of the medial and lateral portions of the marginal ridge being short and parallel and arising at right angles to the apodemal region of the plate, as in *Andrena* (Fig. 1) and the Diphaglossinae (e.g. Fig. 3F).

In *Stenotritus* the lateral portion of the marginal ridge is at a slightly acute ( $80^\circ$ ) angle to the apodemal region but the medial part is at an obtuse ( $\sim 140^\circ$ ) angle, making the whole structure unusually broad (Fig. 2C). The 7th hemitergite of *Hesperapis* is also broad, although rounder in aspect, but this is achieved by increasing the angle between apodemal and lateral portions of the marginal ridge to approximately  $115^\circ$ .

In *Protoxaea* the lateral portion of the marginal ridge is weakly developed, becoming evanescent less than halfway between the apodemal region and the spiracle (Fig. 4C). Indeed, in this taxon this part of the marginal ridge is so weakly developed its existence was only confirmed after examination of the other Oxaeinae in which it is somewhat more strongly developed. The lateral portion is also largely effaced in *Euherbstia* whereas in *Megachile* it is effaced anteriorly, but well-developed in the posterior half (Fig. 5B). Conversely, the lateral portion is unusually strongly developed as an internal shelf-like structure in *Crawfordapis* (Fig. 3F) and even more so in *Lonchopria*.

In most taxa the medial portion of the marginal ridge is fairly straight (Figs 3F, 4D) or gently concave (as in Fig. 5B). It is particularly strongly concave in *Chilicola* and *Protandrena* (Figs 3E, 4A) and unusually short and concave in *Fidelia* (Fig. 5A). In some bees it is bisinuate, concave anteriorly and convex posteriorly, as in *Hylaeus* and *Dasypoda* (Figs 3D, 4E), whereas in *Orphana* it is weakly, and in *Protoxaea* more strongly convex (Figs 2B, 4C). In the apids *Ctenoplectra*, *Exomalopsis* and *Leiopodus*, the posterior end of the medial portion of the marginal ridge is curved laterally at the apex (Fig. 5F). In *Manuelia* the apex of the medial portion is sharply bent apically, more or less at right angles, towards the lateral ridge. In some taxa, the medial portion of the marginal ridge is markedly shortened, being three quarters as long as its lateral portion or less. This situation is found in some Fideiines (Fig. 5A) and particularly in the Melittidae. A more extreme situation is found in *Macropis* and *Meganomia* (Fig. 4F) where the medial portion barely extends beyond the apodemal region, and in *Macrotera* (Fig. 4B), *Alocandrena* and *Megandrena* it is missing entirely beyond the apodemal region.

Another exception to the more usual, approximately equal length of medial and lateral portions of the marginal ridge is found in *Euryglossa*. In this taxon the lateral portion of the marginal ridge is prolonged and

this, together with an extension of the adjacent portion of the lamina spiracularis, forms a digitiform process (Fig. 3C) which is dorsally convex in apical view. A similar but flatter structure is seen in *Scrapter* and *Amegilla*. Conversely, in *Fidelia* and to a lesser extent in all three genera of Lithurgini, the posterior margin of the lamina spiracularis is considerably produced medially (Fig. 5A), such that the two hemitergites almost meet. This situation is not considered to be homologous to that in pemphredonines: in the wasps it is the sclerotized antecostal ridges that converge (here thought to be homologous with the medial portion of the marginal ridge) and these are separate from the lamina spiracularis for most of their length (Fig. 3B). Conversely, in the Fideiines, the sclerotized medial portion of the marginal ridge is very short (approximately one third as long as the lateral portion) and it is the extensions of the laminae spiraculari that converge medially.

There is a laminar extension to both medial and lateral portions of the marginal ridge on the sides opposite to the lamina spiracularis in *Nomada*, *Epeolus* and *Xylocopa* (Fig. 5C,D). The lateral extension is probably homologous to the lateral lamella (see below). These extensions also extend posteriorly and in *Xylocopa* surround the spiracle, which is more posteriorly positioned in this taxon than is usually the case. In *Leiopodus* there is a postero-medial extension of the medial portion of the marginal ridge which seems to support the expanded lamina spiracularis (Fig. 5F). There is a more anteriorly situated external laminar extension to the medial portion of the marginal ridge in *Hylaeus* (Fig. 3D) and all other Hylaeinae observed, but not in *Chilicola* or, apparently, other Xeromelissinae (Aravena & Toro, 1985). The laminar extension of the medial region of the marginal ridge may be homologous with the acrotergite of preceding terga.

In those taxa without any unusual development of the lateral and medial portions of the marginal ridge, the posterior margin of the lamina spiracularis is usually fairly straight (Figs 3F, 4D) or slightly convex (Fig. 3E). It is strongly convex in *Alocandrena* and the Oxaeinae (Fig. 4C), and noticeably concave in *Orphana* (Fig. 2B) and *Systropha*. In all of the Melitidae observed, with the exception of *Hesperapis* and *Haplomelitta*, the lamina spiracularis is unsclerotized along the medial margin posteriorly. This is generally associated with a reduction in the length of the medial portion of the marginal ridge, although in *Dasyopoda* this is almost of normal length (Fig. 4E). In *Macropis* the reduction of the lamina spiracularis occurs right to the medial margin of the spiracular atrium and in *Meganomia* the reduction is so great that the mesal apodeme of the spiracle and the medial 1/4 of the spiracular atrium are not covered (Fig. 4F).

An even greater reduction of the lamina spiracularis occurs in some Andrenidae. In *Megandrena* the spiracle is at the posterior margin of the lamina spiracularis and appears fused to the apex of the lateral portion of the marginal ridge but is otherwise completely surrounded by unsclerotized membrane. This situation is taken even further in *Macrotera* in which the spiracle is more centrally located in the plate, entirely surrounded by unsclerotized membrane (Fig. 4B), and much of the lateral and medial portions of the marginal ridge are missing.

The surface of the lamina spiracularis is modified in a variety of ways. In the Megachilini and all Osmiini observed except *Ochreriades*, there is a marked protrusion of the lamina spiracularis near the base of the lateral process (Fig. 5B). This blister-like feature varies in the extent to which it protrudes and its medial margin may form a quite acute angle projecting medially from the lamina spiracularis; it has not been observed in any other group of bees. The surface of the lamina spiracularis is very weakly microreticulate in many bees (e.g. Fig. 4D) but markedly so only in *Trachusa* (Fig. 2E). Unique to *Cadeguala* is a small perforation of the lamina spiracularis adjacent to the apodemal region half way across the plate. In *Stenotritus* and the Oxaeinae the surface of the lamina spiracularis is setose, particularly posterior to the spiracle (Fig. 4C). This region is similarly clothed in *Trachusa* and Andreninae with marked sting reduction (*Megandrena* and *Alocandrena*). The panurgine *Macrotera* has setae more anteriorly situated, although they are still towards the apex of the considerably reduced sclerotized region of the lamina spiracularis (Fig. 4B).

The spiracle is located near the centre of the lamina spiracularis in most bees and all of the wasp exemplars. It is more posteriorly located in those taxa with a narrow lamina spiracularis, as in all Apidae (e.g. Fig. 5E). In bees with particularly narrow posterior margins of the lamina spiracularis the spiracle may be in contact with both the lateral and antecostal ridges, as in *Epeolus* and *Xylocopa* (Fig. 5C,D). In the latter, the spiracular atrium projects laterally beyond the marginal ridge. The spiracle is also posteriorly situated in *Euryglossa* and *Leiopodus* (Figs 3C, 5F). In *Mydrosoma* it extends somewhat beyond the posterior margin of the lamina spiracularis. The spiracle is situated just anterior to the posterior margin of the plate but close to the lateral portion of the marginal ridge in *Andrena*, *Orphana* (Figs 1, 2B) and *Systropha*, whereas in *Chilicola* and *Dieunomia* it is in contact with the lateral ridge (Figs 3E, 4D). Only in the Lithurgini and *Trachusa* (Fig. 2E) does the spiracle come much closer to the medial portion of the marginal ridge than to the lateral one.

The shape and orientation of the spiracular atrium

also vary. It is comparatively small and approximately circular, forming a simple annulus around the spiracular opening in *Nomada* and *Fidelia* (Fig. 5A) and the apoid wasp *Pemphredon* (Fig. 3B). It is larger with the anterior margin flat or concave in the other wasp and bee exemplars (as, for example, in Figs 3C, 5E). The long axis of the atrium is transverse in *Xylocopa* and *Eucera* (Fig. 5D,E), but rotated slightly postero-laterally in other bees (as in Fig. 4D,E), most strongly so in *Orphana* (Fig. 2B), whereas in *Hylaeus* it is postero-medially rotated (Fig. 3D).

In most bees the morphological orientation of the spiracular opening is dorsal or postero-dorsal. Modifications such that the opening is directed entirely posteriorly have been achieved in two ways. The hemitergite may be longitudinally curved, convex dorsally, with the spiracle closer to the posterior margin, as in *Protandrena*, *Megachile*, *Leiopodus* (Figs 5B,F), *Nomada* and *Xylocopa*. Alternatively, the spiracle may open into the anterior surface of a depression on the hemitergite, as in *Dieunomia*.

Most bees have two apodemes that arise from the spiracular atrium, although all the wasp exemplars with the exception of *Sphex* and *Philanthus* have only one. Note that in many of the figures the apodemes are orientated sufficiently strongly ventrally to make it impossible to see their true shape from the dorsal perspective provided. The lateral apodeme is the one that is universally present and in bees it is longer and more robust as is the case for the apodemes of the spiracular atria of the more anterior terga. The larger lateral apodeme may be elongate and digitiform, as in *Euryglossa* (Fig. 3C) and *Chilicola*, shorter and more robust, as in *Pararophites* and *Fidelia* (Fig. 5A), or bent, like a hooked thumb, as in *Crawfordapis* (Fig. 3F) and *Eucera*. The orientation of the lateral apodeme is also highly variable, being perpendicular to the plate in *Nomada*, orientated anteriorly as in *Crawfordapis* (Fig. 3F) or more medially as in *Dasy-poda* and *Fidelia* (Figs 4E, 5A). The medial apodeme is usually much shorter, often being barely any longer than it is broad, as in *Protoxaea* (Fig. 4C); it is tiny in *Colletes*, *Leioproctus* and *Stenotritus* (but not *Ctenocolletes*) and absent in *Macropis*. However, in the exemplars of Andrenidae and Halictidae it is approximately twice as long as broad (e.g. Fig. 4A). Both apodemes are very long (four times longer than broad) in *Macrotera* (Fig. 4B); perhaps this is required for structural strengthening in the absence of any sclerotization of the lamina spiracularis immediately surrounding the spiracle in this genus.

Unique to the Oxaeinae is a spout-like projection of the outer rim of the spiracle, particularly posteriorly. This can be seen in Figure 4C as the posterior margin to the spiracular opening is somewhat out-of-focus because it projects upwards from the plane of the 7th

hemitergite. The 6th gastral segment has a similar, but much less marked, modification of the spiracle in the Oxaeinae.

The lateral process varies considerably in length; it may even be entirely absent, not only in taxa with extreme sting reduction, as in *Megandrena*, but also in those with comparatively well-developed stings such as *Lonchopria*. The process is comparatively long in *Protandrena* and *Dieunomia* (Fig. 4A,D) but is reduced to a short bump-like protrusion in *Orphana*, *Epeolus* and *Xylocopa* (Figs 2B, 5C,D), *Nomada* and *Trachusa*. In the Oxaeinae and Stenotritidae the process curves posteriorly and may form the lateral margin of the lateral lamella for a considerable proportion of the lamella's length (Figs 2C, 4C).

The shape of the lateral process is quite variable. For example, it appears like a skeletal finger in *Hylaeus* (Fig. 3D), whereas in the Nomiinae and Halictinae it is broadly triangular at the base then narrowing, becoming almost needle-like apically (Fig. 4D). In *Meroglossa* the process is flattened at right angles to the plate as if it were forming an articulatory surface.

The position and orientation of the process in relation to the marginal ridge are highly variable. In most bees the process is approximately at right angles to the lateral portion of the marginal ridge (as in Figs 3C, 4A,D,F, 5E). The process may appear as a simple lateral extension of the apodemal portion of the marginal ridge if it arises anteriorly, as in *Andrena* and *Crawfordapis* (Figs 1, 3F) – taxa with more square-shaped 7th hemitergites. In some taxa in which the hemitergite is strongly U- or V-shaped, the process may be strongly directed posteriorly, again appearing as a continuation of the apodemal portion of the marginal ridge. This is the case in *Colletes*, *Megachile* and *Leiopodus* (Fig. 5B,F) as well as in some pemphredonine wasps (Fig. 3B). In *Hylaeus*, *Ctenoplectra* and *Exomalopsis* the process is similarly posteriorly directed, but does not appear as a continuation of the apodemal portion of the marginal ridge because the latter is more or less linear with respect to the lateral ridge (Fig. 3D). Conversely, in *Chilicola* the process is branched and the broadest portion is slightly anteriorly directed (Fig. 3E). In the exemplar of *Leioproctus*, and also in *Eulonchopria*, it is entirely anteriorly directed, appearing as an anterior extension of the lateral portion of the marginal ridge past the apodemal margin. In *Macrotera* the lateral process is also anteriorly orientated but it clearly is not an anterior extension of the lateral portion of the marginal ridge, which is considerably reduced (Fig. 4B).

The lateral process often bears a short angulation that serves as a site for muscle attachment. In *Dasy-poda* this apodeme is almost as large as the rest of the

greatly reduced process (Fig. 4E) and in *Alocandrena* it appears as if only the apodeme remains. In *Dieunomia* the apodeme is a long, blade-like extension along the long axis of the lateral process (Fig. 4D). The relative position of this apodeme varies, in *Ctenoplectra* it is near the base of the process whereas in *Eucera* and *Leiopodus* (Fig. 5E,F) it is right at the tip, giving the process a forked appearance. In most bees it occupies an intermediate position (Fig. 4D,E).

The lateral lamella is subtended by the lateral portion of the marginal ridge and the lateral process. It is usually about one half as wide as the lamina spiracularis itself (Figs 3B–F, 4F, 5A), but in *Megachile* (Fig. 5B) it is as wide, and in *Dieunomia*, *Eucera* and *Leiopodus* (Figs 4D, 5E,F) much wider than the lamina spiracularis. In each of these except *Dieunomia* this is partly due to the narrow nature of the lamina spiracularis rather than the absolute width of the lamella itself. The lamella is more linear, narrow and parallel to the lateral portion of the marginal ridge in *Andrena* (Fig. 1) and very narrow throughout its length in *Orphana* and *Dasypoda* (Figs 2B, 4E). The lamella usually becomes gradually narrower posteriorly with the outer margin slightly convex, but it varies in shape quite considerably. In *Dieunomia*, for example, it extends laterally, beyond the apex of the lateral process, in a long arc, gradually curving posteriorly and then medially where it extends beyond the apex of the marginal ridge (Fig. 4D). The lateral margin of the lamella is concave in *Chilicola*, *Protandrena* and *Fidelia* (Figs 3E, 4A, 5A), and *Systropha*. In the apids *Nomada*, *Epeolus* and *Xylocopa* (Fig. 5C,D), as mentioned earlier, the lamella is unusually strongly developed posteriorly and in the latter extends beyond the posteriorly located spiracle. In *Crawfordapis* the lamella is absent anteriorly but appears as a strong flange towards the posterior margin (Fig. 3F).

The 7th hemitergite of *Ctenocolletes* is unique in so many features that establishing the homologies of the various parts was only possible upon considering the relative positions of the large and small apodemes of the spiracular atrium. Consequently, this taxon is considered separately here. The 7th hemitergites of *Ctenocolletes* are heavily sclerotized and convex in comparison to other bees (Fig. 2D), notably in comparison to its closest relative, *Stenotritus* (Fig. 2C). The medial portion of the marginal ridge is set at an angle of 135° to the apodemal region, its apex is expanded into a large auger-shaped process and the lamina spiracularis is unsclerotized along its entire medial margin. The lateral portion of the marginal ridge is only ridge-like for its central portion with a weakening of the sclerotization anteriorly, and where its apex should be there is a small concavity in the lamina spiracularis. What appears to be the lateral lamella is bent mesad at right angles to the main axis of the

hemitergite and the lateral process is short, ill-defined and forms the anterior margin to the lamella.

## 8TH HEMITERGITE

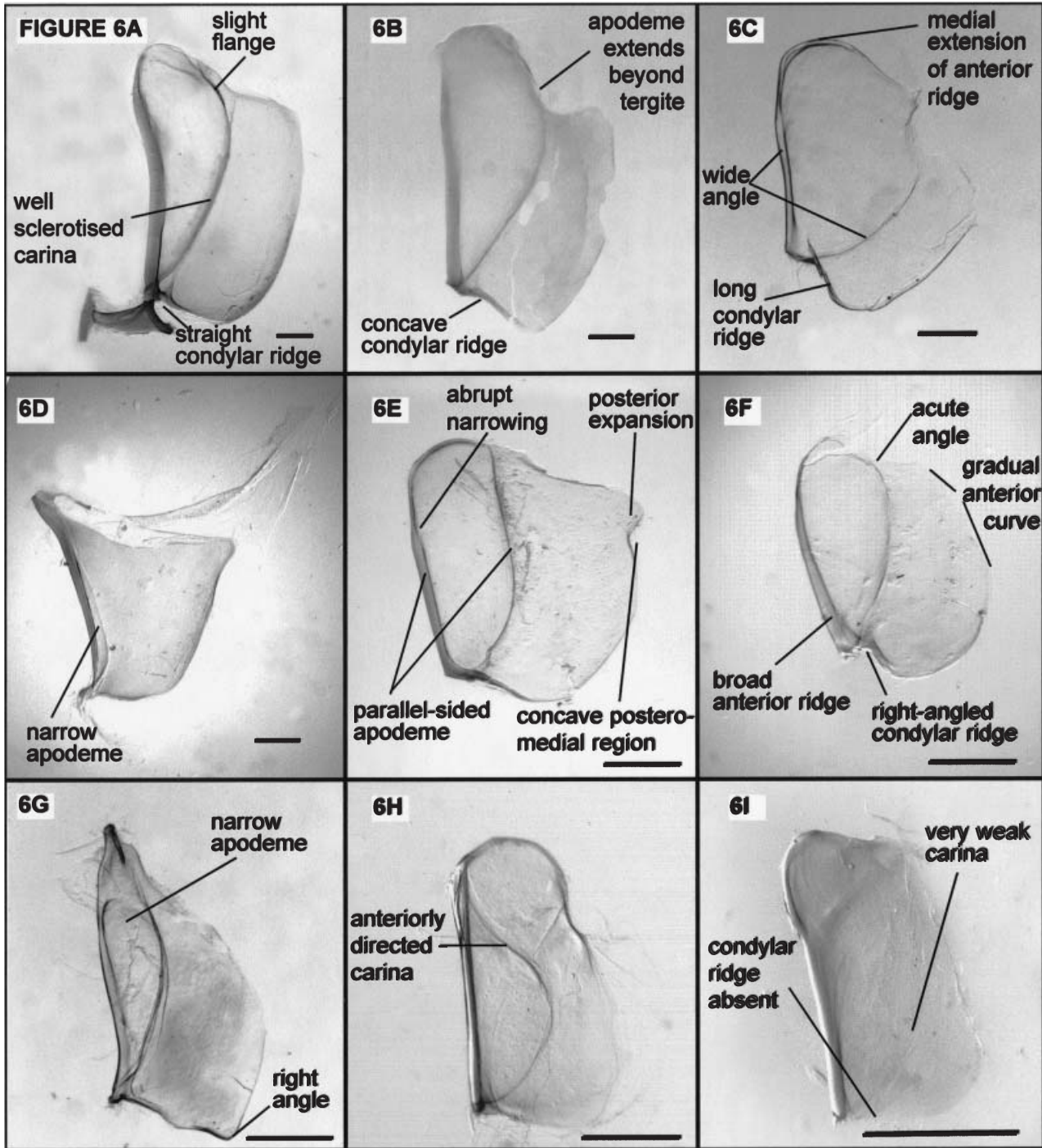
### *Basic structure*

The 8th gastral tergum of bees is divided into two hemitergites, each of which bears an apodeme. The overall structure of the 8th hemitergite is rather simple (Figs 1, 6). Assuming the apodeme to be homologous with those of more anterior segments, it would be attached to the anterior margin of the hemitergite. This view is supported by observations of a bridge between the hemiterga close to where the plate and apodeme meet in several apoid wasp exemplars (e.g. Fig. 8A); this is presumably homologous to the antecosta of the preceding gastral terga. Due to posterolateral rotation of the structure in the evolution of the sting apparatus, as is also the case with the 7th hemitergite, the morphologically anterior margin is orientated dorsally and the lateral margin is ventral. Nonetheless, the morphologically anterior margin is referred to as such. Thus, in this morphologically correct orientation, the apodeme projects anteriorly from the anterior margin of the hemitergite (Figs 1, 6).

The hemitergites themselves are outwardly convex and not heavily sclerotized. They are usually without strong marginal sclerotized ridges, except laterally just behind the condyle where the apodeme of the 8th hemitergite articulates with the dorsal angle of the first valvifer. This stronger lateral margin is termed the condylar ridge. The junction of the hemitergite with the apodeme is usually concave and in the form of a weak carina, although it is often slightly more heavily sclerotized than the disc of the plate. However, as this sclerotized margin often continues along the medial margin of the apodeme continuous with the apodeme's anterior ridge, it appears more like a part of the apodeme than of the plate itself. The posterior margin of the plate is generally slightly convex, whereas its medial margin close to its junction with the apodeme is highly variable (see below). The comparatively strongly sclerotized lateral margin of the plate usually extends postero-laterally for a distance approximating 1/4 of the total width of the plate, with the condylar ridge usually becoming effaced close to where the margin of the plate curves postero-medially.

The apodeme is often approximately semicircular in shape but usually narrower laterally and wider medially, thus appearing somewhat almond-shaped. The anterior margin of the apodeme is heavily sclerotized and forms a ridge, here termed the anterior ridge, which is usually quite straight but which curves abruptly to the posterior at its medial extremity. The ridge continues posteriorly along the medial margin of





**Figure 6.** Variation in 8th hemitergites of bees, morphologically dorsal views anterior to the left. Scale bar = 0.25 mm. (A) *Crawfordapis*, 8th hemitergite and first valvifer. (B) *Caupolicana*. (C) *Protandrena*. (D) *Protoxaea*. (E) *Corynura*. (F) *Melitta*. (G) *Dasypoda*. (H) *Epeolus*. (I) *Leiopodus*.

the apodeme for a variable distance. This continuation rarely continues all the way around the medial margin of the apodeme to make contact with the carina at the junction between hemitergite and apodeme. In these

instances the apodeme is entirely encircled by a marginal ridge. There is a strongly sclerotized lateral condyle to the apodeme which articulates with the dorsal angle of the first valvifer and, as noted above,

continues along the lateral margin of the hemitergite as the condylar ridge.

A very weakly sclerotized remnant of the disc of the 8th tergum is sometimes found in a postero-medial position with respect to the 8th hemitergites. Because this structure is so weakly sclerotized and difficult to discern, it is not dealt with further here.

#### Variation

In *Anoplius* the 8th tergum is not completely divided, and there is a broad sclerotized connection between the two halves and the junction between each plate and this connecting piece is at right angles. The connecting piece has a longitudinal ridge medially, and anterior and posterior ridges on either side. The anterior ridge would seem to be homologous with the antecosta of preceding segments. This set of ridges completely surrounds a more weakly sclerotized oval area on each side. The entire structure has the appearance of an upside-down pair of spectacles, especially when combined with the extension of the antecosta between apodeme and hemitergite, which would form the arms of the spectacles on each side. In *Dolichurus*, there is a fine, heavily sclerotized bridge between the hemitergites at this point, whereas in *Heterogyna*, *Sphex*, *Philanthus* and *Mellinus* (Fig. 8A) the bridge is thicker, intermediate between the situation in *Anoplius* and *Dolichurus*. In the bees the 8th tergum is completely divided into two hemitergites, as it also is in some apoid wasps such as *Tachytes*. However, in *Tachytes* each hemitergite bears a sclerotized mesal projection, apparently homologous to the connection in *Anoplius*, but these do not meet (Fig. 2A). There is an apparently homologous medially directed extension of each hemitergite in the bee genera *Lonchopria* and *Ctenocolletes*. *Xylocopa* has a narrow sclerotized strip extending medially in the same position.

The carina separating the hemitergite from the apodeme is usually evenly curved such that the posterior margin of the apodeme is convex. The apodeme gradually broadens from its lateral margin until close to its medial margin (Fig. 6A–C). This is not the case in *Epeolus*, in which the junction of the hemitergite and apodeme is strongly curved anteriorly one third of the distance from the condyle and reaches the anterior ridge of the apodeme before its medial extremity (Fig. 6H). In *Corynura* the carina is linear and parallel to the anterior ridge for the medial-most 2/3 of its length (Fig. 6E), whereas in *Caupolicana* it is straight for the lateral 2/3 (Fig. 6B). In *Leiopodus* the carina is extremely weak and difficult to detect (Fig. 6H). The carina is often stronger close to its medial extremity. This is most clearly developed in *Crawfordapis* and *Corynura* (Fig. 6A,E), in which it is produced into a small flange.

The relative sizes of the hemitergite and apodeme vary considerably. This variation can best be understood in terms of the angle subtended by the anterior margin of the apodeme and the carina that separates the apodeme from the hemitergite: the more acute the angle, the smaller the apodeme becomes relative to the size of the hemitergite. In most bees the carina is at an angle of between 40° and 60° to the anterior ridge of the apodeme and the hemitergite and apodeme are subequal in area (Fig. 6A,B,F). However, in *Protandrena* (Fig. 6C) the angle is closer to 70° and the apodeme is the larger of the two parts. Conversely, the anterior ridge and carina form a very acute angle in *Meganomia* and an even more acute one in *Dasypoda* (Fig. 6G), in which the apodeme joins the hemitergite at a very acute angle at each end. The smaller size of the apodeme is particularly marked in bees with sting reduction, as in *Stenotritus* and the Oxaeinae (Figs 2C, 6D), in which the apodeme is little more than a narrow rim. In all Oxaeinae observed except *Oxaea* the apodeme is bent ventrally approximately at right angles to the hemitergite throughout its length. In *Leiopodus* the hemitergite is unusually small, being considerably shortened medially such that the entire structure is oblong (Fig. 6I).

In *Trachusa* the 8th hemitergite is markedly convex, bulging outwards (Fig. 2E). Another unique feature of this taxon is the strongly microreticulate surface of the hemitergite; the apodeme, however, is completely devoid of surface sculpture, as it is in other taxa.

In most bees the lateral margin of the hemitergite, extending postero-laterally from the condylar region, is at first concave and then straightens or becomes convex (e.g. Figs 1, 6B,C). However, in *Melitta* (Fig. 6F), *Dieunomia*, *Eucera* and *Xylocopa* it abruptly forms a concave right angle at the base, and the hemitergite extends more laterally than in most other taxa as a result. Alternatively, the lateral margin of the plate may appear as a linear continuation from the basal condyle of the apodeme. This may be approximately at right angles to the anterior margin of the hemitergite, as in *Dasypoda* (Fig. 6G), or at right angles to the anterior margin of the apodeme, as in *Crawfordapis*, *Epeolus* and *Leiopodus* (Fig. 6A,H,I). In most bees the lateral extremity of the hemitergite curves gradually posteriorly and then medially (as in Fig. 6A,F), although in *Dasypoda* (Fig. 6G) it forms a right angle and in *Eucera* a slightly acute one.

The postero-medial margin of the 8th hemitergite usually curves gradually anteriorly towards the hemitergite's junction with the apodeme (as in Fig. 6F). However, it may be extended posteriorly near its medial extremity, with the result that the posterior margin is somewhat concave here and the medial mar-

gin of the hemitergite is longer. This situation is found in *Protoxaea* (Fig. 6D) and in the Nomiinae and Halictinae (Fig. 6E).

The medial margin of the hemitergite forms an acute angle of 45° or less with the apodeme in most bees (Fig. 6A,F,G). In *Tachytes*, *Pemphredon*, *Meroglossa* and *Macropis* the medial margin of the hemitergite joins the posterior margin of the apodeme at a right angle, removed from the apodeme's median extremity. This medial reduction of the hemitergite is most extreme in *Caupolicana* (Fig. 6B) where the apodeme and hemitergite meet at a point over 1/3 of the apodeme's width from its medial edge.

The anterior ridge of the apodeme is parallel-sided throughout most of its length in most bees. However, in *Melitta* it is unusually wide basally, narrowing gradually towards the medial margin (Fig. 6F), whereas in *Corynura* (Fig. 6E) it is more abruptly narrowed. The anterior ridge is straight in most bee genera and forms a rounded right angle with its medial extension, as in *Protandrena* and *Corynura* (Fig. 6C,E). However, there is a slight anterior expansion of the ridge near its medial end in *Chilicola*, *Hylaeus* and all Fideliines except *Pararophites*, and a much larger expansion in *Nomada*. The whole anterior margin is gently concave in *Crawfordapis* (Fig. 6A). Conversely, in *Melitta* it is evenly convex (Fig. 6F) and in *Oxaea* and *Dasygoda* bisinuate, convex laterally, concave medially and the apodeme is spindle shaped (Fig. 6G).

The sclerotized ridge behind the condyle varies in length from extending to the posterior margin of the hemitergite, as in *Protandrena* and *Dasygoda* (Fig. 6C,G), to being entirely absent in *Leiopodus* (Fig. 6I).

As was the case for the 7th hemitergites, the 8th hemitergites of *Ctenocolletes* are unique and very different in structure from that in any of the other bees (Fig. 2D). Because establishing homologies among the parts with those of other bees is unusually difficult, positional information is given both in terms of absolute orientation (outer, inner, etc.) as well as the morphologically correct positions as used elsewhere in this paper. Each hemitergite is comparatively well sclerotized, very convex and its profile in dorsal and ventral views is clearly triangular. The outer (morphologically anterior) and posterior (morphologically medial) margins of this triangle are quite straight, the former giving rise to the apodeme which is large and bent dorsally at right angles to the hemitergite. The inner (morphologically lateral) margin is bisinuate, slightly concave in the posterior half, where the gonostyli pass, and convex anteriorly. The apodeme is depressed inwardly in the middle of its morphologically anterior margin. There is an apical extension beyond the medial margin of the apodeme and plate which

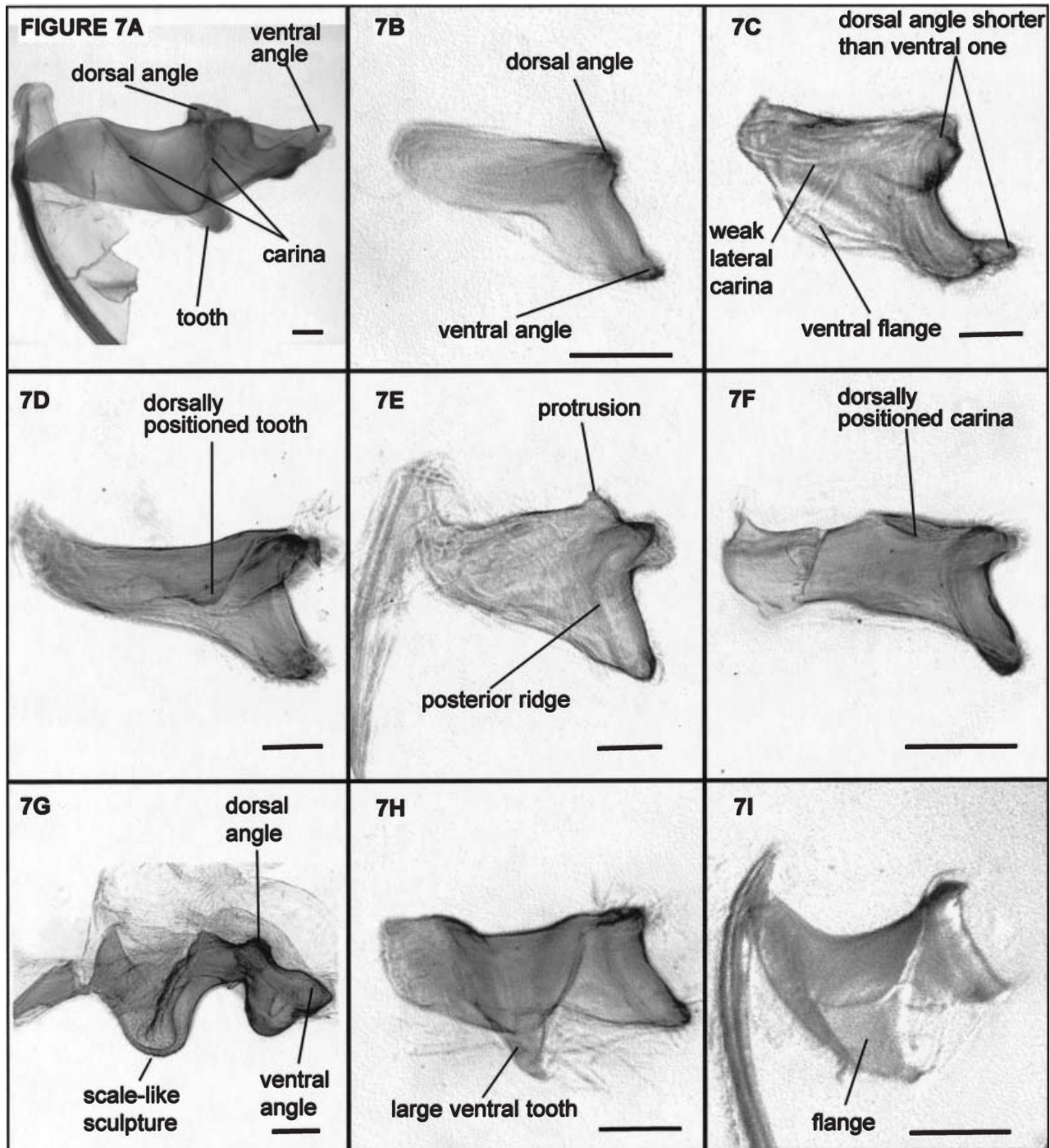
appears homologous to the bridge between the plates found in *Anoplius* and some apoid wasps (see above). In dorsal view the anterior margin of the apodeme is very irregular and forms four convexities, one either side of the medial depression, and two apical to the medial ridge.

#### FIRST VALVIFER AND FIRST VALVULA (FIRST RAMUS AND LANCET)

##### *Basic structure*

The first valvifers are small, comparatively robust structures which usually approximate an elongate triangle in shape with the shortest side to the posterior (Figs 1, 7). Each first valvifer gives rise to a first valvula which is termed, in its basal region, the first ramus and, more apically, the lancet of the sting apparatus (Fig. 1). All three parts form a flexible, but firmly constructed, narrow sclerotization. According to Scudder (1961) the first valvifers (which he termed gonangula) are probably derived from the antero-lateral corners of the coxa of abdominal segment IX (i.e. gastral segment 8). Smith (1970) however, considered them as having been derived from the gonocoxites of the 7th gastral segment. The latter seems reasonable considering that both authors suggest that the first ramus is derived from gastral segment 7. No attempt is made here to orientate this small, comparatively simple structure in terms of what may have been its original position, rather, the terms dorsal, ventral, anterior, posterior, etc. refer to the relative positions of the part as it occurs in the insect at rest (Fig. 1).

The dorsal margin of the first valvifer is flat or slightly concave and the ventral one convex, at least anteriorly, such that the structure appears to curve slightly upwards to the origin of the first ramus (Fig. 7). The posterior margin is usually somewhat concave between dorsal and ventral angles (Fig. 7). These angles articulate with the 8th hemitergite and second valvifer, respectively. The ventral angle is generally slightly longer than the dorsal one and its development renders the ventral margin of the first valvifer concave posteriorly. There is usually a posterior ridge appearing as an arc extending for the entire depth of the first valvifer on its inner surface, just anterior to the two angles (Fig. 7E,F). Often there is a longitudinal carina on the outer surface, which may be developed into a tooth (Fig. 7D), less often into a large flange (Fig. 7I). The first valvifer is thinner (lateromedially) close to the origin of the first ramus and then gradually thickens towards the angles. It is at its thickest just ventral to the dorsal angle and just dorsal to the ventral angle, such that its inner surface is concave between the angles when viewed anteriorly or posteriorly.



**Figure 7.** Variation in the first valvifers of bees and wasps, lateral views anterior to the left. Scale bar = 0.1 mm. (A) *Anoplius*, first valvifer with first ramus attached. (B) *Pemphredon*. (C) *Systropha*. (D) *Dieunomia*. (E) *Fidelia*, valvifer with first ramus attached. (F) *Lithurgus*. (G) *Trachusa*. (H) *Nomada*. (I) *Leiopodus*, valvifer with first ramus attached.

Anteriorly, the first ramus is attached to the apex of the first valvifer at approximately a right angle to it. It projects dorsally only very slightly (Fig. 7I). The rest of the ramus is long and thin and directed ventrally and

then posteriorly. It bears a longitudinal, dorsal groove (aulax) along which a corresponding tongue (rhachis) of the second ramus slides (Smith, 1970; Quicke, Leralec & Vilhelmsen, 1999). The first ramus curves pos-

teriorly close to the base of the sting shaft and becomes the lancet (Fig. 1).

The lancet is a long, thin, apically pointed extension of the first ramus. The dorsal surface of the lancet bears a short boss which itself bears a pair of valvilli (Figs 1, 8E) (Quicke *et al.*, 1992) on the dorsal surface. Most aculeate workers have called the boss plus valvilli a valve. The valvilli are housed by the bulb of the sting shaft and the movement of the lancets causes them to push venom along the lumen of the shaft to the exterior (Snodgrass, 1956). The valvilli are thought to be a synapomorphy of the [Aculeata + Ichneumonidea] as they are not found in any of the other Parasitica or Symphyta (Quicke *et al.*, 1992).

#### Variation

There is not a great deal of variation in this comparatively simple structure. In *Anoplius* (Fig. 7A) the first valvifer is elongate with the ventral condyle at the end of a posterior extension and the dorsal one small, such that the two are almost on a straight line with the point of attachment of the valvifer to the ramus. The longitudinal external carina is deeply bowed ventrally and projects beyond the ventral margin of the valvifer as a tooth that is slightly longer than its basal width. In the exemplars of apoid wasps the first valvifer is unremarkable, generally triangular with the dorsal condyle shorter than the ventral one and with (*Tachytes*, *Philanthus*) or without (*Dolichurus*, pemphredonines (Fig. 7B), *Mellinus*) an external longitudinal carina which bears at most a very short tooth. In *Sphex* there is a strong, ventrally directed tooth just anterior to the dorsal condyle.

Among the bees, the length to depth ratio of the first valvifer varies. In *Ctenocolletes* it forms an equilateral triangle, in *Protandrena* it is barely any longer than its greatest depth (Fig. 8E), in *Corynura* (Fig. 9B) it is only 1.5 times longer than deep, whereas in *Orphana* (Fig. 2B) it is more than three times as long as its greatest depth. In other bees its dimensions lie between those of the last two (Fig. 7B–I).

In all Fideliines, including *Pararophites*, the first valvifers appear as simple triangles, with all sides more or less straight and without strongly developed condylar extensions or unusual features, other than a postero-dorsal nipple-like protrusion in *Fidelia* (Fig. 7E). *Systropha* has a thin ventral flange rendering the ventral margin convex (Fig. 7C) whereas, in contrast, *Eulonchopria* has a swelling on the dorsal surface.

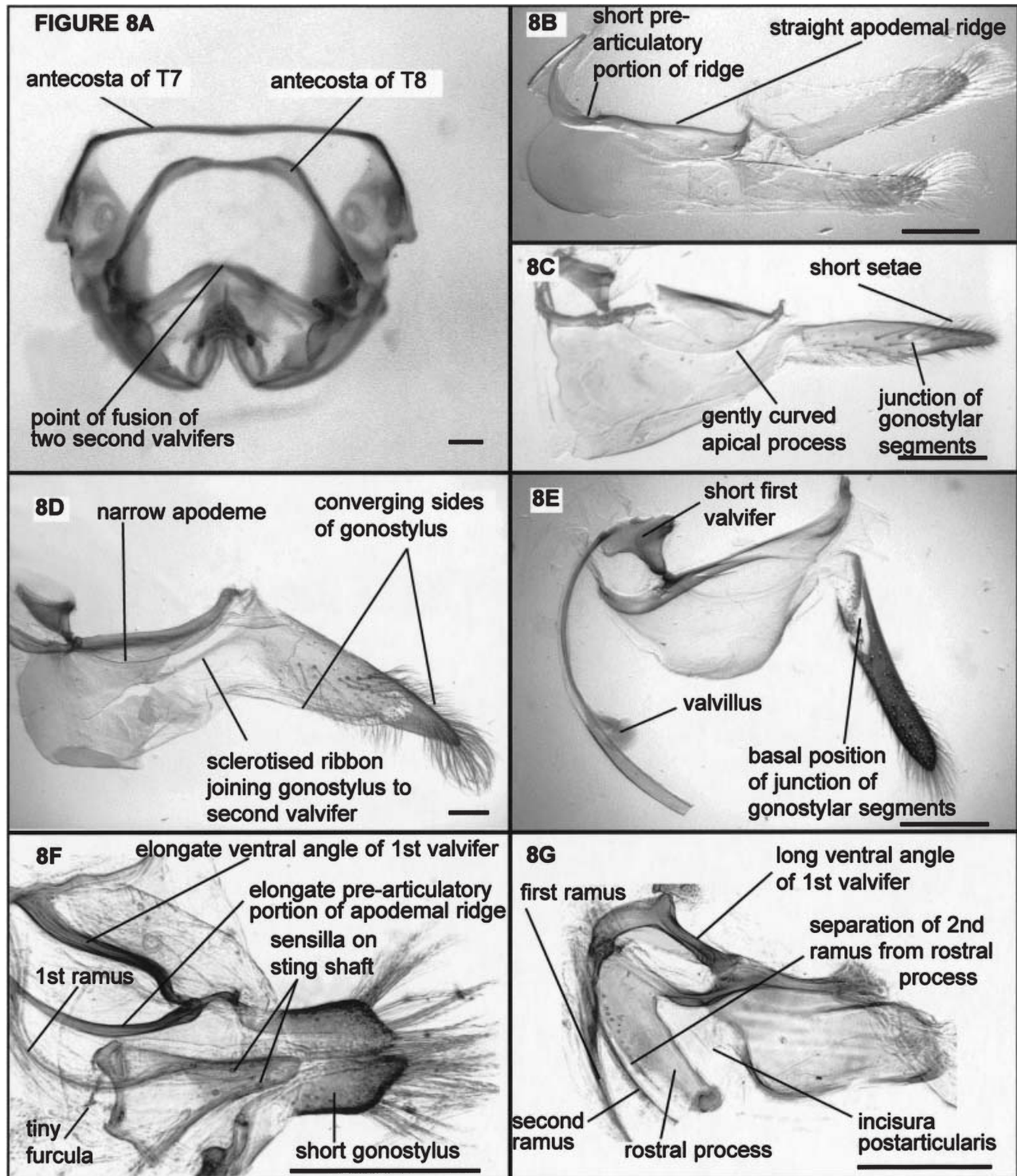
In most bees the dorsal and ventral margins of the first valvifer converge fairly evenly towards the attachment of the first ramus. However, in *Andrena* and *Lithurgus* (Figs 1, 7F) in particular, the ventral margin is ventrally bowed before reaching the ramus,

narrowing only just before the attachment. In *Trachusa* the first valvifer is highly divergent from that of any other taxa (Fig. 7G). In dorsal view, it is strongly bent into a U-shape (Fig. 2E). The inner, anterior extremity representing the ventral angle and the outer, anterior extremity is where the valvifer is attached to the ramus. The area just behind the ventral angle is greatly swollen. The dorsal angle is strongly sclerotized, but is only weakly protuberant. Uniquely, the outer surface of the first valvifer in *Trachusa* is microreticulate, as a result of scale-like sculpture (Fig. 7G).

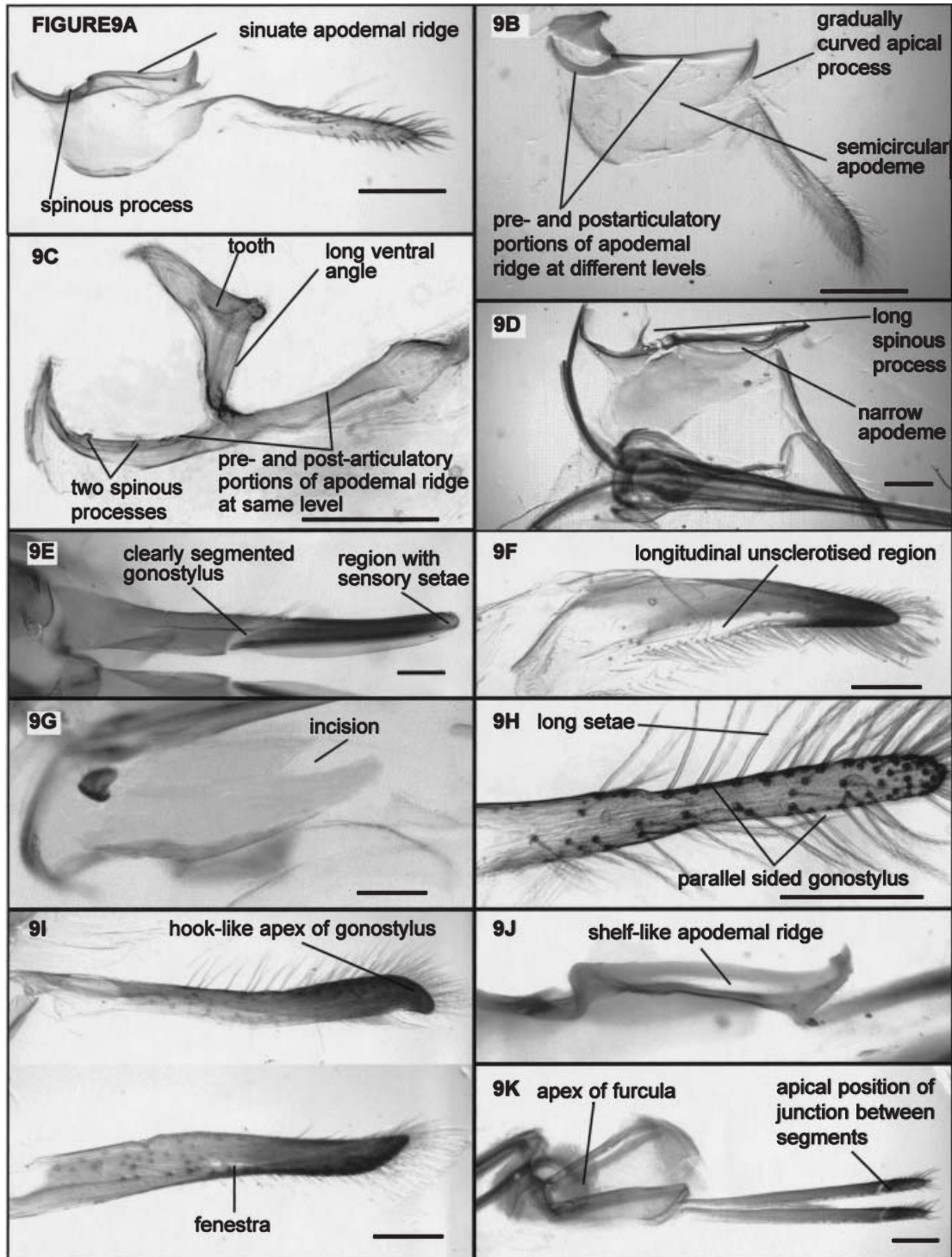
The degree of concavity of the posterior margin of the first valvifer varies. In *Eulonchopria* and *Xylocopa* the posterior margin is straight or almost so, as it is in *Dasygoda* (Fig. 9C). Conversely, in *Stenotritus*, the dorsal and ventral angles and the main body of the valvifer are considerably lengthened, such that the triangular plate appears as a spindly Y-shaped structure (Fig. 2C). In *Oxaea* and *P. (Notoxaea)* the dorsal angle is not produced but the ventral one is very long, longer than the body of the valvifer. In *Protoxaea* the posterior margin is wide, deep and transversely concave forming a scoop-shaped structure (Fig. 8G).

The ventral angle is slightly the longer of the two in most bees as, for example, in *Systropha* (Fig. 8B), but in *Dasygoda* (Fig. 9C) and *Meganomia* the ventral condyle is much longer; indeed, in the former the ventral angle is almost as long as the body of the valvifer. The most extreme condition is in *Macrotera* where the ventral angle is at the end of an enormous extension of the ventral arm of the plate, fully three times longer than the body of the valvifer (Fig. 8F). This is associated with the very long basal concavity of the second valvifer (see below).

If present, the longitudinal carina on the lateral surface of the valvifer is usually weak, but is strongly developed and comparatively dorsally situated in *Lithurgus* (Fig. 7F) and *Trichothurgus* but not *Microthurge*. In some bees the carina is produced into a tooth, this is particularly strong in *Dasygoda* (Fig. 9C), *Macropis* and *Eucera* in which it is close to the dorsal angle. In most other bees which have a lateral tooth it is more ventrally positioned, as in *Ctenoplectra*, whereas in *Dieunomia* it is both more ventral and more anteriorly positioned (Fig. 7D). In the apids *Nomada* (Fig. 7H) and *Exomalopsis*, and also in *Meganomia*, the tooth is so strongly developed as to extend beyond the ventral margin of the plate. In the latter two genera it is also unusually anteriorly positioned. In *Epeolus* the tooth is produced into a large ventral flange, and this is even more strongly developed in *Leiopodus* in which the flange is longer than the greatest depth of the valvifer (Fig. 7I). This flange is not necessarily associated with cleptoparasitism in the Apidae, as some other cleptoparasites have a flange of



**Figure 8.** Variation in second valvifers of bees and apoid wasps, lateral view, anterior to the left unless otherwise stated. Scale bar = 0.25 mm. (A) Whole sting apparatus of *Mellinus*. Apico-dorsal view of sting apparatus to show sclerotized bridges uniting the two 7th hemiterga, the two 8th hemiterga and the second valvifers, ventral surface at bottom of figure. (B) *Euryglossa*, second valvifer. (C) *Hylaeus*, first and second valvifers. (D) *Crawfordapis*, first and second valvifers. (E) *Protandrena*, first and second valvifers with first ramus and base of lancet. (F) *Macrotera*, ventral view of sting shaft, and parts of first and second valvifers. (G) *Protoxaea*, first and second valvifers with gonostylus omitted.



**Figure 9.** Variation in the first and second valvifers or gonostyli of various bees and apoid wasps, lateral views anterior to the left unless otherwise stated. Scale bar = 0.25 mm. (A) *Systropha*, second valvifer. (B) *Corynura*, first and second valvifers. (C) *Dasygoda*, first and part of second valvifers. (D) *Eucera*, second valvifer and sting shaft. (E) *Tachytes*, gonostylus in ventral view. (F) *Colletes*, gonostylus. (G) *Dieunomia*, second valvifer, ventro-lateral view. (H) *Dasygoda*, gonostylus. (I) *Dieunomia*, gonostylus ventral view. (J) *Lithurgus*, anterior ridge region of second valvifer in dorsal view. (K) *Dieunomia*, gonostylus in lateral view. (L) *Coelioxoides*, second valvifer and apex of rami and furcula.

intermediate length (*Coelioxoides*) or none at all (*Osiris*, Fig. 2F).

Variation in the rami is primarily restricted to its reduction in bees with reduced stings and an increase in length in some cleptoparasitic bees. In *Megandrena*, *Alocandrena* and Stenotritidae it arises from the valvifer not at right angles to the latter's longitudinal axis, but rather as an anterior extension (Figs 2C, 8G). In *Alocandrena* the ramus is membranous other than for a very fine sclerotized thread along most of its length and this sclerotization does not make contact with the first valvifer. In contrast, in another Andrenine, *Orphana*, the ramus is extremely broad and very well sclerotized even though it is obvious that the lancets cannot be inserted into the considerably reduced sting shaft (Fig. 2B). At rest, the rami and lancets of this genus curve posteriorly considerably ventral to the sting shaft. In cleptoparasitic apids with long stings, the first rami are often comparatively long. This is most extreme in *Osiris* (Fig. 2F).

Variation in the structure of the lancets is minimal and largely restricted to varying degrees of reduction. In bees with markedly reduced stings (Stenotritidae, Oxaeinae, *Megandrena*, *Alocandrena*; Figs 2C, 7G) the lancets are not housed within the sting shaft and are reduced to narrow ribbons which may be partially or entirely membranous. Similarly, in these taxa, the valvilli and their basal boss are entirely absent (Fig. 2B,C).

The sting autotomy mechanism of worker honey bees is well known and is facilitated by the large barbs in the apical region of the lancets which extend, laterally, beyond the margin of the stylet (Mulfinger *et al.*, 1992). In non-*Apis* bees with serrated lancets, the serrations are usually restricted to the extreme apex of the structure and do not extend beyond the stylet laterally. Poore (1974) surveyed the number and shape of the lancet barbs in 37 species of bees. He found the barbs to be readily detectable in all species except one (*Anthophora curta* Provancher) and that most bees had barbs that were acutely tipped, whereas only *Nomada* and one of two species of *Andrena* had rounded barbs, and only *Melissodes* had intermediate, saw-toothed barbs. Poore (1974) found the number of barbs to vary only by  $\pm 1$  within species but to vary considerably among them. His tables indicate that most individuals of all species of Halictidae had seven barbs, the Megachilidae had six or seven, with the exception of *Lithurgus* which had two or three, as did *Andrena*, *Bombus* and also queens of *Apis*. The other Apidae (*sensu* Roig-Alsina & Michener, 1993) had between one and three barbs, with the exception of a few individuals of some species of *Diadasia* (four), *Centris* (4–6), and *Apis* workers which had more barbs than any other bee (10–12).

I have found the number of lancet barbs in the

wasps to vary between 15 in *Anoplius* to three in *Philanthus* and *Pemphredon*, with the other taxa having a maximum of six. Almost all of the bees had three lancet barbs, usually situated at the extreme apex of the lancet. The only bees with more than three barbs were *Fidelia* and *Corynura* with five each. Reduction in the number of barbs was more common: *Andrena*, *Systropha* and *Eucera* had two; *Macropis* and *Xylocopa* had one, *Orphana* had one strongly developed barb (visible as a more strongly sclerotized spot in Fig. 2B). No lancet barbs were found in the cleptoparasitic Apidae, bees with marked sting reduction and membranous lancets, and *Meganomia*. The slight differences between numbers reported here and those obtained by Poore (1974) presumably result from somewhat different taxa being used in the two studies.

#### SECOND VALVIFER, SECOND VALVULA AND GONOSTYLUS

##### *Basic structure*

Of all the sting sclerites, the second valvifers lie closest to the sting shaft itself and, other than the sting, are the most ventrally positioned parts of the entire apparatus (Figs 1, 11F). Each is a complex structure bearing an apodeme, the second ramus and gonostylus (Fig. 1). As is the case with other parts of the sting apparatus, the orientation of the second valvifer has changed greatly in the course of its evolution. According to Smith (1970), the gonostylus arises from the lateral and the second ramus from the mesal surface of the second valvifer. In position within the insect they are posterior and anterior, respectively. According to Smith's orientation, the apodeme would be posterior to the valvifer itself whereas *in situ* it is dorsal to the plate. As the second valvifer is a posteriorly directed appendage, it is morphologically correct to state that the ramus arises basally and the gonostylus is apically situated. As this is also their position with respect to the valvifer within the insect at rest, these less formal terms of orientation are used.

The main body of the second valvifer is outwardly convex and generally more weakly sclerotized than the other parts of the sting apparatus, often being membranous along its inner margin. The second valvifer is unsclerotized around the base of the gonostyli except for a narrow ribbon that links the two structures in most bees (e.g. Fig. 8D).

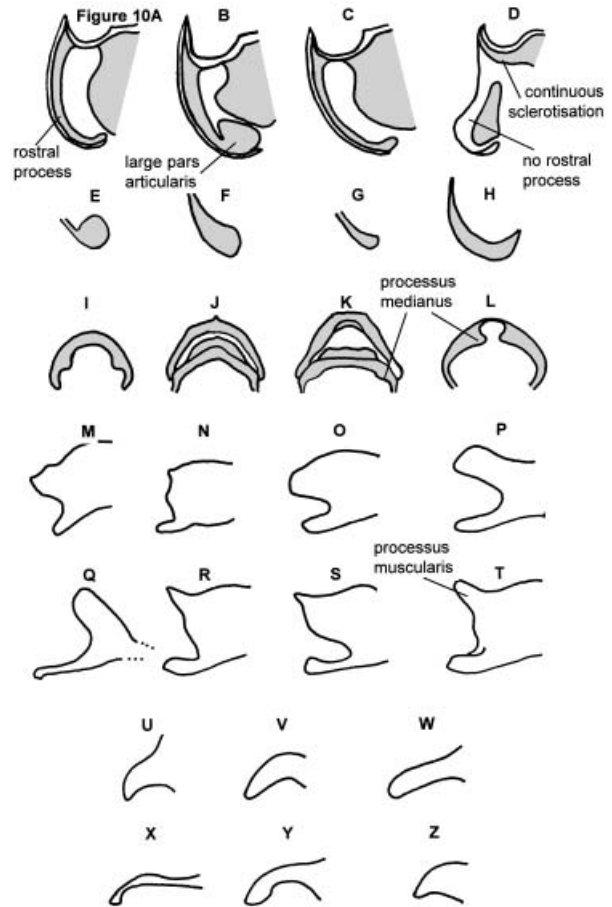
The apodeme is somewhat outwardly concave. It is fused to the second valvifer for most of its length but has an apical free portion called the apical process which is separated from the plate by a narrow incision, here termed the apical cleft (Fig. 1). The lower margin of the apodeme is gently convex and its junction with the second valvifer and the lower margin of the apical process form one continuous curve. The



upper margin of the apodeme is thickened as a ridge, here termed the apodemal ridge of the second valvifer. In most taxa (Figs 8B,C, 9B, but not *Andrena* in Fig. 1) this apodemal ridge is straight for most of its length but is reflexed upwards at the tip of the apical process, where it forms a narrow process which is slightly developed both inwardly and outwardly. Basally, the ridge continues past the apparent basal extremity of the apodeme and becomes strongly concave with the extreme tip recurved apico-dorsally. The junction between straight and concave regions of the anterior ridge is marked by an angle, here termed the articular condyle of the second valvifer (Fig. 1), which articulates with the ventral angle of the first valvifer. There is a small hair plate of trichoid sensilla (Hermann & Douglas, 1976) usually just below the condyle (Figs 1, 8E) and often one, rarely two (Fig. 9A,C, respectively), small processes, here termed the spinous processes of the second valvifer, arising from the dorsal margin of the concavity. The condyle can be considered as separating pre- and post-articulatory portions of the apodemal ridge (Fig. 9B,C).

The strongly recurved basal portion of the apodemal ridge is fused on its outer edge to the base of the second ramus and both then curve, first downwards then apically, in a long arc towards the base of the sting shaft (Fig. 1). It is along this curved portion that the second ramus forms a sliding interlock with the first ramus. The posterior margin of the second ramus is usually attached to a long, narrow sclerotized strip called the rostral process (Fig. 10A–C). At its ventral apex, the rostral process is expanded to form the pars articularis (Fig. 10A–C) which articulates with the processus articularis at the base of the sting shaft. The rostral process is at least partially separated from the main body of the second valvifer by a deep incision arising from the ventral margin of the plate, which is called the incisura postarticularis (Fig. 1). At its apex the incisura postarticularis may attain the lower margin of the concave, prearticulatory portion of the apodemal ridge. The incisura postarticularis is narrowest adjacent to the pars articularis, then widens before finally narrowing towards its dorsal extremity (Fig. 1).

The gonostyli appear approximately cylindrical, but each is in fact made up from a long, narrow sheet of sclerotization which is curled into a tube with the innermost margin largely membranous or appearing as a separate area of weaker sclerotization. The attachment of the gonostylus to the body of the second valvifer is immediately ventral to the apical cleft (Fig. 1). The base of the gonostylus is usually membranous and this region has been shown to be involved with the secretion of an alarm pheromone in honey bee workers (Cassier, Tel-Zur & Lensky, 1994). However, it is not known whether it has a glandular function in



**Figure 10.** Basal portions of second valvifers (A–D), sting shafts (E–T) and processus articularis (U–Z), anterior to the left unless otherwise stated. (A–D) Incisura postarticularis and adjacent structures of (A) *Euryglossa*, (B) *Diphaglossa*, (C) *Systropha*, and (D) *Nomada*. (E–H) Pars articularis of (E) *Caupolicana*, (F) *Crawfordapis*, (G) *Andrena*, (H) *Megachile*. (I–L) Anterior views of sting shaft bases, dorsal to the top, of (I) *Colletes*, (J) *Andrena* (with furcula), (K) *Melitta* (with furcula), and (L) *Exomalopsis*. (M–T) Lateral view of sting shaft base of (M) *Tachytes*, (N) *Hylaeus*, (O) *Eulonchopria*, (P) *Diphaglossa*, (Q) *Oxaea*, showing entire sclerotized portion of sting shaft, base of membranous region dotted, (R) *Dieunomia*, (S) *Megachile*, and (T) *Xylocopa*. (U–Z) Ventral view of processus articularis of (U) *Tachytes*, (V) *Diphaglossa*, (W) *Macropis*, (X) *Oxaea*, (Y) *Eucera*, and (Z) *Xylocopa*.

any other bees. The gonostylus of *Apis* certainly appears more membranous than in the bees surveyed here and bears extremely few setae in comparison. Poore (1974) divided the sting sheaths of the Aculeata into five categories: (i) unsegmented, (ii) constricted medially without clearly separate segments, and (iii–v) clearly divided into two segments. In category

(iii) these segments are of the same length, whereas in category (iv) the basal one is twice as long, and in (v) approximately half as long as the apical one.

#### Variation

The two second valvifers are connected by a narrow, heavily sclerotized bridge in *Anoplius*, *Heterogyna*, *Tachytes* and *Mellinus* (Fig. 8A). This arises medially from the apex of the apical process and traverses the sting apparatus just dorsal to the sting shaft. A bridge was not found in any of the other apoid wasps or bees surveyed, although a short but strong medially directed angulation is seen in *Sphex* and, as noted below, many bees have a very small extension of the apical process here. However, in the bees this angulation is often outwardly directed in part or in its entirety.

The apodemal ridge of the second valvifer may only be a slight thickening, as in some Colletidae such as *Euryglossa* (Fig. 8B) and *Colletes*, or it may be developed as an internal ridge as in the Andrenidae and *Xylocopa*. Alternatively, it may be an externally developed ridge as in the Hylaeinae, the Halictinae and *Epeolus*. In all Megachilidae except *Coelioxys* and the Fideliinae, the external ridge is very strongly developed and forms a flattened shelf, set off at an acute angle from the rest of the apodeme and increasing in width towards the tip of the apical process (Fig. 9J).

The post-articulatory portion of the apodemal ridge is usually straight (Figs 8B,C,E, 9B,D) but is somewhat concave in *Colletes*, *Crawfordapis* (Fig. 8D), *Lonchopria* and *Andrena*, and sinuate in *Systropha* (Fig. 9A). At its deepest point, the apodeme varies from one half to as deep as the depth of the adjacent portion of the valvifer, narrowing both basally and apically such that it is approximately semicircular (Figs 8C, 9B). Exceptions are *Lonchopria* and *Andrena* in which the concave post-articulatory portion of the apodemal ridge results in the apodeme being narrow basally, broadening gradually to the apical process which is the widest part (Fig. 1). In *Crawfordapis* and *Eucera* the apodeme is approximately one quarter as deep as the rest of the valvifer, again a result of the concave apodemal ridge, but the overall shape of the apodeme is more normal in these genera (Figs 8D, 9D). In *Systropha* the junction between apodeme and plate is somewhat sinuous, more or less parallel to the similarly shaped apodemal ridge (Fig. 9A). In *Stenotritus*, *Oxaea* and *Protoxaea* (*Notoxaea*) the apodeme is minute, strongly sclerotized and linear; in *P. (Protoxaea)* it is minute but of normal shape. In *Ctenocolletes* the only sclerotized part of the whole second valvifer is a narrow, heavily sclerotized structure which is apically forked, with the inner fork presumably representing the apical process (Fig. 2D).

Viewed from the side, the apical process of the apodeme varies in shape. In most taxa its lower margin is abruptly angulate at the extreme apex, forming a sharp process as in the apoid wasps and *Euryglossa* (Fig. 8B). Sometimes this margin slopes in a gentle curve to the apex, as in *Hylaeus* and *Corynura* (Figs 8C, 9B). *Melitta* has a uniquely uneven apex to the free portion of the apical process which appears almost as if eroded away, and in *Dasypoda* the apex of the apical process is twisted such that it is horizontal, appearing to provide a basal support for the gonostylus. In *Alocandrena* the apical process is no more than a narrow extension of the sclerotized apodemal ridge with a tiny knob at its apex.

In posterior view, and when viewed apically, the extreme apex of the apical process is usually slightly flared both inwardly and outwardly. However, in *Tachytes* (Fig. 2A), *Systropha* and *Fidelia* the apex is largely inwardly directed, whereas in *Chilicola*, the Hylaeinae, *Pararophites* and *Lithurgus* it is only outwardly developed (Fig. 9J). Conversely, in the Pemphredoninae and some bees such as *Dieunomia* and *Melitta* there is no expansion in either direction.

The apical cleft is uniquely long in *Euherbstia*, almost reaching the concave section of the apodemal ridge whereas, in contrast, it is completely missing in *Megandrena* (see below).

The relative proportions of the pre- and post-articulatory portions of the apodemal ridge vary among bees. The concave pre-articulatory portion is relatively long, up to one half the length of the entire ridge in the Stenotritidae and Oxaeinae (Figs 2C, 8G), and also those Andrenines with reduced sting apparatuses and unusually small second valvifers, such as *Orphana* (Fig. 2B). The most extreme condition is found in *Macrotera* in which the concave pre-articulatory portion is three times as long as the post-articulatory part (Fig. 8F). Conversely, it is short, one third as long as the entire ridge, in *Colletes* and *Euryglossa* (Fig. 8B). The concavity varies in depth. It may be barely noticeably concave, continuing past the articulatory condyle at the same level as the post-articulatory portion, as in Colletidae (Fig. 8B–D), *Dasypoda* (Fig. 9C), *Melitta* and the Fideliinae. Conversely, it may be markedly concave, as in *Corynura* (Fig. 9B) and *Dieunomia*, although in most bees the concave portion is of intermediate depth. In *Trachusa*, the concave portion of the apodeme is horizontal in orientation, strongly sclerotized and unusually broad, appearing as a large, semicircular keel (Fig. 2E).

The spinous process from the upper margin of the prearticulatory portion of the apodemal ridge is particularly marked, being at least twice as long as broad in *Pemphredon*, *Fidelia* and *Megachile*. It is particularly long in some species of *Lithurgus* and in *Eucera*, where it is fully five times longer than wide, projects

apically, and is unusually narrow (Fig. 9D). In *Xylocopa* and *Exomalopsis* it is located more medially and posteriorly and seems to prevent inward movement of the ventral angle of the first valvifer. It is a particularly broad and robust structure in the latter taxon. All other bees observed either have a small angle (*Crawfordapis*, *Cadeguala*), a small triangular projection (*Meganomia*, *Trachusa*, *Epeolus*), an almost square stub (*Eulonchopria*, *Systropha*; Fig. 9A), or no projection at all (most of the remaining taxa). Uniquely, *Dasypoda* has two narrow processes (Fig. 9C).

The incisura postarticularis is delimited by the rostral process anteriorly and the anterior margin of the main part of the second valvifer posteriorly (Fig. 1). Its anterior margin is usually curved and largely parallel to the second ramus, except where separated from the latter by the pars articularis. Its posterior margin is more variable depending upon the shape of the main body of the valvifer here, which is usually convex and somewhat parallel to the second ramus such that the incisura postarticularis is also parallel-sided (Fig. 10A). Exceptions include *Meroglossa* and *Melitta* in which the anterior margin of the body of the valvifer is biconcave, making the incisura postarticularis deeply biconvex posteriorly. In *Systropha* the basal margin of the main body of the valvifer is very convex such that the incisura postarticularis widens abruptly (Fig. 10C) as it also does in the Diphaglossines, although in the latter this expansion also results from the broad pars articularis (see below; Fig. 10B).

The dorsal apex of the incisura postarticularis is usually on, or close to, the concave pre-articulatory region of the apodemal ridge (Fig. 10A–C). In the apoid wasp *Tachytes* and the Colletid *Calomelitta* the entire lower edge of the pre-articulatory portion of the ridge is free of the sclerotized valvifer and the incisura postarticularis is very wide here. In most bees, the incisura postarticularis meets the anterior ridge for approximately only the basal third of the length of the pre-articulatory portion of the ridge. However, in *Euryglossa*, *Diphaglossa* and *Protoxaea* it is the central third of this concavity which the incisura postarticularis meets (Figs 8G, 10A,B), and in *Lonchopria* and *Caupolicana* it is the central two thirds which is not in contact with the sclerotized valvifer.

Only in *Andrena* (Fig. 1), *Dasypoda*, *Fidelia*, *Megachile*, *Eucera* and *Nomada* does the incisura postarticularis clearly not reach the apodemal ridge but is separated from it by a section of the sclerotized valvifer (Figs 9D, 10D). This sclerotization is usually very narrow, approximating the width of the ramus. Exceptions include *Megachile* in which it is twice the width of the ramus and *Nomada* in which this area of sclerotization is similarly wide but, uniquely, is almost the

only sclerotized portion of the entire non-apodemal part of the valvifer (Fig. 10I).

Unique to the Oxaeinae is an apparently double incisura postarticularis. There is a narrow absence of sclerotization immediately posterior to the second ramus, between the ramus and the rostral process. The second region lacking sclerotization is where the incisura postarticularis is in other bees (Fig. 8G). The most anterior part of the valvifer is expanded ventrally and appears like a pars articularis. However, it is actually the section of the plate between the two incisions, the rostral process, which articulates with the processus articularis of the sting shaft of these bees.

The rostral process is very narrow, bordering on absent, in most of the bees observed, being barely any broader than the second ramus (Fig. 10C). However, it is more strongly developed in *Corynura* and *Meganomia*, in which it is approximately twice as wide as the ramus. In *Euryglossa* and *Diphaglossa* (Fig. 10A,B) it is much wider at its upper end (three times and twice the width of the ramus, respectively), but narrowing to the width of the ramus just before expanding again to form the pars articularis.

The pars articularis is usually small, at its greatest width being only two or three times as wide as the second ramus (Fig. 10A,F), although in *Macropis* and all Diphaglossinae it may be 4–5 times as broad (Fig. 10B,E,F). In *Sphex* and the Pemphredoninae examined, it is enormous, 7–8 times as wide as the second ramus. Conversely, in *Mellinus* the incisura postarticularis is absent and the base of the sting articulates upon a strengthened ridge along the basal-medial margin of the second valvifer. The pars articularis may arise as a very gradual broadening of the rostral process, as in *Chilicola* and *Andrena* (Fig. 10G), or it may be somewhat more abrupt, as in most other bees, particularly in *Mydosoma*, *Cadeguala*, *Caupolicana* (Fig. 10E), *Macropis* and *Ctenoplectra*. In *Diphaglossa* (Fig. 10B) it forms an acute angle with the second ramus and projects antero-dorsally on its upper margin. Alone among the Diphaglossinae, *Crawfordapis* has a gradually expanding pars articularis, but like the other members of the subfamily, it is very broad (Fig. 10F). The apex of the pars articularis is usually rounded (Fig. 10A–F) although it is somewhat flat medio-apically in *Corynura* and *Meganomia* and even concave in *Oxaea*. In *Stenotritus* the pars articularis is a small knob, whereas in *Ctenocolletes* this whole region of the valvifer is largely membranous, although the tiny sclerotized spot near the base of the sting may represent vestiges of the pars articularis. In the Megachilidae and also *Xylocopa* the pars articularis is unusually long and narrow, being particularly large, and sickle-shaped in *Megachile* (Fig. 10H).

A complex of features common to all cleptoparasitic Apidae observed is a reduction in size of the pars articularis, a great expansion of the incisura postarticularis and loss of much of the sclerotization of the main body of the second valvifer, especially basally, such that most of it appears membranous (Fig. 10D).

A unique synapomorphy of the Nomiinae is an acute, basally directed incision in the sclerotization of the inner, ventral margin of the second valvifer. This renders the area immediately apical to the incision appear as an apically directed lobe (Fig. 9G). This has been observed in all exemplars of the subfamily listed in Table 1 but in no other bees, although a shallow concavity in this region is found in *Ctenoplectra*. In *Xylocopa* and *Eucera* the plate is largely membranous along its inner margin.

Variation in the second ramus is minimal although, not surprisingly, it is weakly developed in bees with marked sting reduction but still sclerotized in all of them except *Ctenocolletes*. In *Alocandrena* the second ramus, presumably fused with the rostral process throughout, is strongly sclerotized and seems to form a strut supporting the greatly broadened bulb of the sting shaft. Another unique development is seen in *Megandrena* in which the whole body of the second valvifer is a well-sclerotized but small and simplified structure in which no incisura postarticularis, apical cleft or rostral process can be discerned. However, its postero-medial corner articulates with the base of the sting shaft and this presumably represents the pars articularis.

In *Tachytes*, and to a lesser extent *Philanthus*, the origin of the gonostylus is in an almost socket-like concavity in the second valvifer; this is not the case in bees and the other wasps. Another difference between most bees and most aculeate wasps observed is that in the latter there is no sclerotized band joining the gonostylus with the second valvifer. In most bees, and also the apoid wasp *Pemphredon*, a narrow sclerotized ribbon joins the two structures (Figs 8C,D, 9A). This originates just below the apical cleft and leads to the dorsal region of the base of the gonostylus. However, this narrow sclerotization is missing in the bees *Megandrena*, *Meganomia*, *Xylocopa* and *Epeolus*.

The gonostyli vary greatly in relative length and breadth. They may be up to ten times longer than broad, as in *Coelioxoides* (Fig. 9K), and almost as long in *Lithurgus*, *Neofidelia*, *Meganomia* and *Dieunomia* (Fig. 9I). Conversely, they are unusually short in comparison to their width (length less than or equal to five times their width) in *Euryglossa* (Fig. 8B), *Protoxaea*, *Andrena* (Fig. 1) and *Pararophites*. However, the shortest gonostyli found were among taxa with reduced stings: in *Macrotera* they were only twice as long as broad (Fig. 8F) and the next shortest were in *Orphana* where they were less than three times as

long as broad (Fig. 2B). Thus, moderately short gonostyli are found commonly in bees with reduced stings but are not restricted to them. The gonostyli are much used in the taxonomy of stingless bees (Michener, 1990).

Clear division of the gonostyli into two apparent segments that appear capable of articulation is found in the wasps *Anoplius*, *Dolichurus*, *Sphex* and *Tachytes* (Fig. 9E). The basal segment is markedly convex apically such that the junction between the two is U-shaped when viewed from the side. The segmental nature of the gonostyli is much less clear in the bees and the remaining crabronid exemplars in which the junction between the segments is often marked only by an area of weakened sclerotization and even this may be absent, as in the Halictinae (Fig. 9B), *Macropis* and *Meganomia*. It is also absent in some long-tongued bees such as *Eucera*. In *Neofidelia*, *Ctenoplectra* and *Nomada* the delineation between the two apparent segments is in the form of a very acute V. In *Fidelia*, the Stenotritidae and *Protoxaea*, the junction between segments appears merely as a slight lengthening of the weakened area of sclerotization at the very base of the gonostyli. In *Andrena*, *Protandrena* (Fig. 8E) and *Oxaea* the junction is very basally positioned. Conversely, in *Hylaeus*, *Lonchopria* and *Crawfordapis* it is much more apically located (Fig. 8C,D). The apical position of the junction between segments is most extreme in *Coelioxoides* in which the apical segment is only one-sixth the length of the entire sheath (Fig. 9K).

In some bees the junction between the two segments of the gonostyli is represented solely by a longitudinal weakening. This appears to be an extension of the ventral part of the U-shaped junction between segments, as in *Colletes* (Fig. 9F). In *Crawfordapis* the area of weakened sclerotization is longitudinal for most of the length of the gonostylus but turns abruptly dorsally towards the apex (Fig. 8D). In *Dieunomia* the junction is also longitudinal but is separated from any other area of weakened sclerotization, appearing as a narrow fenestration in the middle of the structure (Fig. 9I).

The gonostyli of *Anoplius* are narrow at the base, widening to the junction between segments and then narrowing again. A similar widening, though less marked, is observed in *Sphex* and the bees *Hylaeus* (Fig. 8C) and *Ctenoplectra*. In most bees, however, the gonostyli are more or less parallel-sided for most of their length, as in *Protandrena* (Fig. 8E). Exceptions include *Colletes* and *Crawfordapis* (Figs 8D, 9F) in which they gradually narrow from close to the base to the apex. The Halictinae have a different shaped apex to the gonostylus which is widest subapically, curving gradually to an almost hook-like apex (Fig. 9B), most strongly so in *Dieunomia* (Fig. 9I). Other unusual conditions are the deep apical incision accompanied by a

dorso-ventral flattening of the apical segment in the wasp *Philanthus*; the somewhat obliquely truncate apices in *Macrotera* (Fig. 8F); the narrow, cylindrical gonostyli of *Dasygaster* (Fig. 9H) which narrow comparatively abruptly at the junction between segments; the evenly, ventrally curved gonostyli of *Xylocopa* and the almost conical gonostyli of *Orphana* (Fig. 2B).

Both segments of the gonostyli bear setae which vary greatly in size, robustness and density. These are generally short and sparse in the spheciform wasps, which also have a cluster of sensilla situated in a fingernail-shaped area of somewhat reduced sclerotization at the tip of the apical segment (Fig. 9E). This specialized patch of sensilla is seemingly absent in bees, as is the more weakly sclerotized apical portion of the gonostylus. Bees have comparatively long setae in this region (Figs 2B,E, 8B-F, 9A,B,F,H,I,K), and the loss of the patch of sensilla may be a synapomorphy for them. In most bees, the setae are either of approximately uniform length, as in *Dieunomia* (Fig. 9I), or they are longer towards the apex, as in *Crawfordapis* (Fig. 8D). Exceptions include *Xylocopa* in which they are longest subapically and *Hylaeus* in which they become shorter towards the apex (Fig. 8C). The setae are usually approximately as long as the width of the gonostylus, although in *Dasygaster* (Fig. 9H) and *Meganomia* they are very long, more than twice as wide as the gonostyli. In Oxaeinae and *Orphana*, the apical setae are very long, up to 2/3 of the length of the gonostylus (Fig. 2B) and in *Macrotera* they are as long as the gonostylus (Fig. 8F; although in these bees the gonostyli are comparatively short). Conversely, in *Hylaeus* most of the setae are only approximately half as long as the width of the gonostylus (Fig. 8C).

The setae are usually denser in the apical half of the gonostylus and may even form a tuft at the apex, as in *Crawfordapis* (Fig. 8D), *Melitta* and *Exomalopsis*, whereas in *Trachusa* (Fig. 2E) they are so dense apically as to make the gonostylar apex appear felt-like. Conversely, in *Systropha* and *Coelioxoides* (Fig. 9A,L) they are notably sparse throughout.

The setae are apically directed at an angle of less than 45° to the long axis of the gonostylus. In most bees, the apical setae are also divergent; however, the few long hairs at the apex in *Leiopodus* are entirely parallel to the long axis of the gonostylus. The setae are more divergent than usual in *Dasygaster* (Fig. 9H), *Pararophites* and *Neofidelia*.

#### STING SHAFT (= FUSED SECOND VALVULAE)

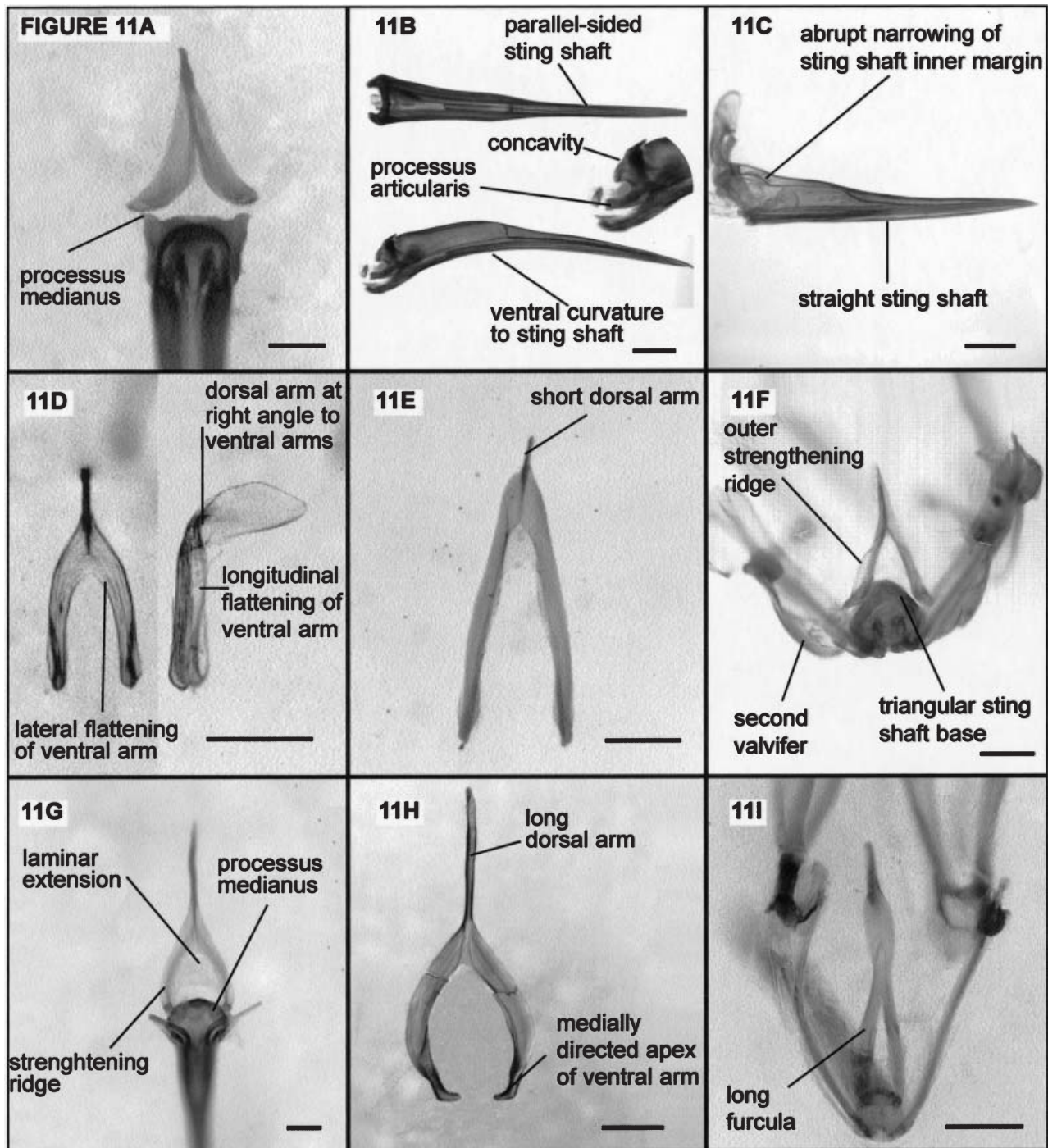
##### *Basic structure*

The second valvulae are fused dorsally to form the sting shaft. Ventrally their position is taken up by the lancets except when the sting is reduced and non-functional. Basally, the shaft is expanded laterally and

dorsally into a bulb, which varies in length relative to that of the narrower, more apical stylet. In lateral view, the inner surface of the bulb can be seen to narrow to the stylet abruptly and more anteriorly than does the outer surface (Fig. 11B,C). The bulb is often noticeably narrower internally than externally, the difference in width being greatest approximately half way along its length (Figs 1, 11B). The sting shaft is usually straight or slightly curved ventrally (Fig. 11B,C). The anterior region of the bulb is particularly heavily sclerotized, forming a basal ring. In the wasps there are angulations arising from the anterior margin of the sting shaft serving as points of articulation with the furcula, each of these projections is termed a processus medianus (Fig. 11A). These are absent or reduced and orientated more medio-ventrally in bees, such that they are rarely visible in dorsal or ventral view but can be seen when viewed anteriorly (Figs 10J-L, 11G). The anterior opening of the shaft is approximately circular but with the inner margin produced latero-ventrally as a result of the change in orientation of the two processi mediani (Fig. 10I,K,L). On each side of the ventral margin of the sting shaft base there is a small, anteriorly orientated projection, the processus articularis, onto which the pars articularis of the second ramus articulates (Fig. 1). There is a hair plate in the middle of the processus articularis. Just dorsal to the processus articularis there is an incision, here termed the basal incision of the sting shaft (Fig. 1). The dorsal anterior margin of the sting shaft may be slightly produced as a rim, which is called the processus muscularis (Oeser, 1961; Fig. 10R). There are scattered sensilla on the sting shaft (Fig. 8F).

##### *Variation*

On each side of the anterior margin of the sting shaft in *Anoplius* and the apoid wasps there is an angulate projection which is orientated anteriorly, this is the processus medianus (Fig. 11A). It is strongly developed in all of these wasps except *Sphex* and *Mellinus*, in which it is small, but distinct. In the bees these structures are somewhat reduced and usually medio-ventrally produced rather than anteriorly directed, and thus partially occlude the anterior opening of the sting shaft (Figs 10I,K,L, 11G). These processes are only visible in dorsal view in the Colletidae (Fig. 11B), *Andrena*, *Melitta* (Fig. 10K), *Meganomia*, *Trachusa* and some of the cleptoparasitic Apidae, and in these bees they are smaller than in the wasps. The processes are not visible in dorsal view, but are clearly detectable projecting into the lumen of the sting shaft base when this is viewed from the anterior in the remaining bees (Figs 10I,K,L, 11G). In those bees in which the processes are visible dorsally this is at least partly a



**Figure 11.** Variation in structure of the furcula and sting shaft in the Apoidea, viewed from the anterior unless otherwise stated. (A) *Tachytes*, showing articulation of furcula with the processi mediani on each side of the sting shaft base, ventral view with furcula rotated anteriorly. (B) *Colletes*, showing dorsal and lateral views of sting shaft with inset enlarged view of sting shaft base, anterior to left. (C) *Hesperapis*, lateral view of sting shaft and furcula, anterior to left. (D) *Hylaeus*, anterior and lateral views of furcula. (E) *Colletes*, furcula. (F) *Macropis*, furcula and base of sting shaft and other sting sclerites, dorsal towards top of figure. (G) *Lithurgus*, furcula and sting shaft base with furcula rotated somewhat anteriorly. (H) *Megachile*, furcula. (I) *Epeolus*, furcula, sting shaft base and portions of sting sclerites, dorsal towards top of figure.

result of the concave dorsal margin of the sting shaft base. This concavity is particularly marked in *Colletes* (Fig. 11B), *Mourecotelles* and *Leioproctus*, in which the anterior margin of the sting shaft is curved medially on each side of the concavity. In *Colletes* the processi mediani are ventrally located in comparison to other bees (Fig. 10I). Unique to *Andrena* is the extreme lateral position of the processus medianus which projects, but only slightly, anteriorly and not at all medially (Fig. 10J). In *Exomalopsis* the processi mediani are very broad and dorsally positioned such that the distance between the two of them is unusually narrow (Fig. 10L).

The general orientation of the open, anterior end of the sting shaft is antero-ventral in the wasps (e.g. Fig. 10M) but more purely anteriorly in most bees (Fig. 10N–T). The exceptions are those bees with marked sting reduction in which the whole ventral surface of the sting shaft may be open (Fig. 2C,D).

In anterior view, the base of the sting usually approximates an upside-down U-shape (Fig. 10I,L), with the lancets forming the more flattened ventral margin. The depth and breadth of the sting shaft are approximately equal anteriorly, as in *Colletes* (Figs 10I, 11B), although in *Meganomia* the base of the sting shaft is broader than deep. In *Macropis* the dorsal margin of the sting shaft is produced such that in anterior view it is almost triangular (Fig. 11F), whereas in *Dasygoda* a pentagon is formed.

The basal incision of the sting shaft bulb is approximately parallel-sided in lateral view and twice as long as deep in most bees (Fig. 10O,S). It appears comparatively deep in some bees, this being achieved in two different ways. In *Mourecotelles*, the Diphaglossinae and *Dasygoda* it is simply a broader incision (Fig. 10P), whereas in taxa with a more strongly developed processus muscularis the greater depth is achieved by a more gradual slope starting from a more anteriorly produced dorsal margin (Fig. 10Q,R). The latter situation is found in *Lonchopria*, *Dieunomia* and the long-tongued bees. Only in these taxa is the processus muscularis really evident as a process: a short lip such that, in profile, the dorsal region of the base of the bulb appears slightly concave (Fig. 10R–T). In *Colletes* this margin is also concave but, uniquely, it slopes antero-ventrally towards the antero-dorsal margin of the basal incision (Fig. 11B).

The processus articularis is slightly flattened and its long axis is orientated more or less horizontally in most bees, somewhat more diagonally in the wasps. *Dasygoda* has the least horizontal orientation among the bees, and in the long-tongued bees the base of the processus articularis is often slanted, arising more ventrally on the sting shaft, and the processus articularis becomes orientated more horizontally by mid length.

The shape of the processus articularis in ventral view is usually somewhat digitiform (Fig. 10W), although in *Melitta*, *Nomada* and *Xylocopa* it is more triangular with a broad base (Fig. 10Z). It is slightly expanded towards the apex in *Lonchopria*, *Trachusa*, *Ctenoplectra* and *Eucera* (Fig. 10Y). The relative length of the processus articularis is also variable. Its length equals its basal width in the apoid wasp *Tachytes* (Fig. 10U) and it is only one and a half times as long as wide in *Lonchopria* and *Chilicola*. In all other wasps, and also in all other Colletidae (Fig. 10V) except *Colletes*, it is approximately twice as long as wide. In *Colletes*, Halictidae, Andrenidae (other than those with extreme sting reduction) and most Melittidae it is three times longer than broad, whereas in long-tongued bees other than *Lithurgus* and *Xylocopa* (Fig. 10Z) it is generally at least four times longer than broad (Fig. 10W). In the Oxaeinae, the processus articularis is comparatively long and narrow with an outwardly directed, more heavily sclerotized, triangular apex which articulates with the second valvifer (Fig. 10Q,X).

In lateral view, the tip of the processus articularis is usually directly below the anterior-most point of the base of the sting shaft bulb, excepting the processus muscularis, if present (Fig. 10P,S). However, its short length and more ventral orientation in the wasp *Tachytes* means that its apex is posterior to the anterior margin of the bulb (Fig. 10M). The processus articularis does not reach the anterior-most margin of the base of the bulb in *Eulonchopria* (Fig. 10O) and the Diphaglossinae, whereas in *Hylaeus* and *Colletes* it extends beyond the base of the bulb (Figs 10N, 11B).

In profile, the dorsal surface of the sting shaft bulb is slightly concave in most bees (Figs 1, 2F), its inner margin more strongly so, although both are barely noticeably concave in the Colletidae (except *Chilicola*; Fig. 11B), *Dasygoda* and the long-tongued bees. In some taxa the bulb is constricted twice, once close to the base and then again at its apex; this is most noticeable for the inner margin of the bulb and is most marked in *Hesperapis* (Fig. 11C). In *Ctenoplectra* and *Xylocopa* the outer surface of the bulb is gently convex in profile.

The bulb of the sting shaft is greatly expanded and widely open ventrally in those bees with marked sting reduction (Figs 2C,D, 8F). At its most extreme, the bulb may be so expanded in comparison to the shaft that the whole structure is wider than long, as in *Alocandrena* (see Michener, 2000, fig. 49-2). In *Oxaea* only the basal ring of the sting shaft remains sclerotized (Fig. 10Q), in the other Oxaeinae the rest of the sting shaft is very weakly, but noticeably, sclerotized.

In most bees, the junction between the bulb and stylet of the sting is marked by a slight constriction of the sting shaft as viewed ventrally or dorsally, as in

*Colletes* (Fig. 11B). This is most marked in *Corynura* and *Xylocopa*. In contrast, there is a much more gradual narrowing of the sting throughout in the apoid wasps, *Diphaglossa*, *Andrena* (Fig. 1), the Melittidae (except *Hesperapis*) and *Nomada*. In *Coelioxoides* the narrowing of the sting shaft is so gradual as to make recognition of the distinction between bulb and stylet difficult (Roig-Alsina, 1990, fig. 13a). *Coelioxoides* and *Osiris* have a subapical swelling to the stylet half way or more along its length (Fig. 2F). The stylet usually narrows gradually to its apex, although it is comparatively parallel-sided until close to its apex in *Colletes* (Fig. 11B) and *Epeolus*. It is usually approximately circular in cross-section, being only noticeably deeper than wide in *Corynura*, *Macropis*, *Nomada* and *Xylocopa* and shallower than wide in *Protandrena*. The bulb is usually 2/3–4/5 as long as the stylet (Fig. 11B). It is longer in *Andrena*, in which the short stylet is barely any longer than the sting bulb (Fig. 1). Conversely, the bulb is short, half as long as the stylet in *Chilicola* and *Dasypoda*.

The relative length to breadth of the sting shaft is highly variable. With the exception of those taxa with marked sting reduction, the relatively shortest stings are found in *Lonchopria*, *Andrena*, *Corynura* and *Melitta*, in which the sting approximates six times its width (as measured just posterior to the basal thickening of the structure). Particularly long stings (ten times longer than their near-basal breadth) are found in *Crawfordapis*, *Dieunomia* and all exemplars of Megachilinae and Apidae listed in Table 1, except *Trachusa* and *Xylocopa*. Very long stings, 15 times longer than broad, were found in *Nomada* and *Coelioxoides* (Roig-Alsina, 1991) and the longest was in *Osiris* which has a sting fully 20 times longer than broad (Fig. 2F).

The sting shaft is strongly curved ventrally in all wasps observed, except the pemphredonines in which it is weakly curved or straight. In the bees it is dorsally curved only in *Systropha* and here only very weakly so. Otherwise it is straight or slightly decurved, most strongly so in *Colletes* (Fig. 9B), the Diphaglossinae and *Melitta*, whereas in *Dieunomia*, *Pararophites* and *Xylocopa* it is bent ventrally somewhat abruptly at the junction of the stylet and bulb. Aravena & Toro (1985) found variation in the curvature of the sting shaft among genera of Xeromelissinae.

#### THE FURCULA

##### Basic structure

Articulating on either side of the sting shaft base and orientated dorsally from there is a wishbone or tuning fork-shaped sclerotization called the furcula. The stem of the Y has been referred to as the dorsal arm and the

two other arms as the ventral arms of the furcula (Fig. 1; Hermann & Chao, 1983). The tips of the ventral arms of the Y articulate on either side of the base of the sting shaft, towards the dorsal surface. In lateral view, the dorsal and ventral arms usually form a gentle curve and the dorsal arm is orientated more posteriorly, often paralleling the sting shaft. The dorsal arm in particular is laterally compressed (Fig. 11D). Variation in this structure among the major groups of aculeate Hymenoptera, with particular reference to ants, was surveyed by Hermann & Chao (1983) and it has been figured in various groups of cleptoparasitic Apidae by Roig-Alsina (1989, 1991).

##### Variation

Despite its structural simplicity, the furcula exhibits a remarkable diversity of shapes. The relative sizes of the dorsal and ventral arms, their relative thickness, the degree of curvature of the ventral arms and the shape of the dorsal arm as seen laterally are highly variable features.

In the wasps *Anoplius*, *Dolichurus* and *Sphex* the furcula is rather small, robust and V-shaped with a short dorsal arm and a small lumen between the ventral arms and the base of the sting shaft (Fig. 11A). Among the bees, a similarly shaped furcula is found only in *Ctenocolletes*, a genus with sting reduction in which the furcula is very small and detached from the sting shaft base. In the remaining apoid wasps studied, the furcula is somewhat less robust, still triangular but with a somewhat longer dorsal arm, the latter being most strongly developed in *Philanthus*, in which the dorsal and ventral arms are subequal. The furcula is comparatively larger in bees, usually with more space between the ventral arms and the base of the sting shaft (Fig. 11D–I).

In most bees the articulation between furcula and sting shaft is approximately half way up the sides of the anterior margin of the sting shaft base (Fig. 11G). However, the point of attachment is more dorsal in taxa with short and widely divergent ventral arms, such as Oxaeinae, *Andrena*, *Macropis* (Fig. 11F) and *Dasypoda*. Particularly in *Macropis* (Fig. 11F), the ventral arms are outwardly bent apically such that their inner surfaces are flush with the base of the sting shaft. Conversely, a more ventral articulation is found in some of the taxa with long ventral arms, particularly in the Megachilinae (except the Lithurgini) and the Halictid *Dieunomia*. In all Megachilinae except *Coelioxys*, the apex of each ventral arm is bent medially to form the articulation, this is most marked in *Megachile* (Fig. 11H).

The area subtended by the arms of the furcula is usually slightly smaller than the area of the base of the sting shaft but it may be considerably larger, as in



*Colletes*, *Hylaeus*, *Dieunomia* and Megachilinae (except Lithurgini) and Apidae (Fig. 11D,E,H). In all three genera of Lithurgini this area seems to be large, but upon close examination most of the space can be seen to be filled by a thin lamina which leaves only a short opening close to the base of the sting shaft (Fig. 11G). *Leiopodus* has a similar broad lamina to the furcula, although the inner margin of the lumen in this genus is somewhat longer. In the remaining cleptoparasitic Apidae the ventral arms are long and more parallel, leaving a long but narrow (as in *Nomada* and *Epeolus*, Fig. 11I), to very narrow lumen, as in *Osiris* (Fig. 2F) and *Coelioxoides*.

Especially in bees with reduced stings, the furcula is often small and the dorsal arm in particular has a tendency to be lost. This yields a variety of simplified shapes such that the furcula is like a curly bracket (⌋) in *Megandrena* and *Andrena* (Fig. 10J), a more square-shaped bracket (⌋) in *Euherbstia* and *Stenotritus* (Fig. 2E) and a simple U in *Melitta* (Fig. 10L). The furcula is unusually small and narrow throughout in *Euherbstia*, an Andrenid without marked sting reduction. In *Alocandrena* the only part of the furcula that remains is a small, sclerotized disc on either side of the sting base where the furcula would be expected to articulate with the sting shaft. The furcula is also greatly reduced such as to be barely detectable in *Macrotera* in which it remains vaguely Y-shaped (Fig. 8F).

In cross-section, the ventral arms may be rounded, as in most short-tongued bees. However, in all long-tongued bees they are antero-posteriorly flattened (Fig. 11G,H), strongly so in all taxa except *Trachusa*. In the Apidae, the ventral arms are somewhat twisted apically so as to appear laterally compressed just before their articulation with the sting base. This twisting appears necessary to permit their articulation. A strengthening internal ridge is found in many of these taxa. It is towards the medial margin of the arms in the Fideliinae and most Megachilinae (Fig. 11H), on their outer margin in *Xylocopa* and *Eucera*, but centrally positioned in the Lithurgini (Fig. 11G). The ventral arms are laterally compressed in *Chilicola*, *Systropha* and the Halictinae and particularly strongly so in *Macropis* (Fig. 11F), which has an anterior strengthening ridge projecting outwardly. *Hylaeus* has ventral arms that are curved in cross-section and thus superficially appear both longitudinally and laterally flattened (Fig. 11D).

In most bees, the dorsal and ventral arms are subequal in length. The dorsal arm is much shorter than the ventral arms in *Andrena*, *Colletes* (Figs 1, 11E), *Meganomia*, the Fideliinae, all Apidae except *Xylocopa*, and those taxa with sting reduction noted above. Conversely, the dorsal arm is longer than the ventral arms in the Lithurgini (Fig. 11G) and also *Trachusa*. In the cleptoparasitic apids *Osiris* and *Coelioxoides*

the transition between ventral and dorsal arms is not easy to distinguish because the ventral arms are fused for a considerable proportion of their length. The ventral arms thus form a long strip-like structure before the furcula becomes laterally compressed at the point of origin of the dorsal arm (Fig. 2F). This great lengthening of the furcula in *Osiris* and *Coelioxoides* (it is 2/3 and 1/2 as long as the sting, respectively) seem to enable it to function as a lever permitting the extrusion of the entire sting shaft outside of the body.

In side view, the dorsal arm of the furcula forms an abrupt right angle with the ventral arms in the wasps *Anoplius* and *Philanthus* and in the bees *Hylaeus* (Fig. 11D), *Dieunomia* and *Ctenoplectra*. In the remaining apoid wasps (except *Tachytes*) and most bees, the dorsal and ventral arms form one gradual curve. In *Tachytes*, *Colletes* and *Nomioides* the dorsal and ventral arms are continuous such that the entire structure appears linear in profile. The furcula of *Epeolus* and *Nomada* forms an elongate S in lateral view. The even longer furcula of *Osiris* is much straighter (Fig. 2F), whereas that of *Coelioxoides* gently undulates with the dorsal arm recurved and appearing like the scrolled head of a violin (Fig. 9K; Roig-Alsina, 1990, fig. 13f). In lateral view the dorsal arm may be short and round, as in *Colletes*, bluntly oval but wider towards the apex, as in most taxa, or broadest at mid length, tapering to the apex, as in *Hylaeus* (Fig. 11D) and *Xylocopa*. It is laterally compressed in all taxa in which it is long enough for its shape to be readily detectable, with the exception of the Megachilinae (excepting *Trachusa*) in which it is narrow and approximately cylindrical, and *Neofidelina* (but not other Fideliinae) in which it is narrow but dorso-ventrally compressed.

## DISCUSSION

I have documented a wide range of variation in the structure of all of the skeletal parts of the sting apparatus in bees. The degree of variation is such that many bees which, externally, appear very similar, can be differentiated rather easily based upon characteristics of the sting. Why is it that the sting apparatus of bees is so variable in form?

The sting apparatus of bees may be expected to have diverged from that in their carnivorous apoid ancestors as a result of its having a different suite of functions. The sting apparatus of apoid wasps may be expected to have been under strong selection for the purposes of paralyzing prey, in addition to its more general defensive function. Modifications of the sting apparatus in these insects may be expected to result from variation in the prey utilized and the exact behaviours associated with the stinging action, which is often very precise (see for example, Steiner, 1971;

also Evans & West Eberhard, 1973; O'Neill, 2001). In contrast, the bee sting is not used to paralyse prey, its only function (as a sting) is in defence against potential predators/parasites (or, for cleptoparasites, as a defense against hosts) and in offence against conspecifics, for example, in instances of attempted nest usurpation. Relaxation of selection permitting a wider variety of sting morphologies may be expected to have occurred among the bees. The repeated gross reduction of the sting in bees to the extent that it is no longer capable of functioning as a sting is one indication of this. This loss of sting function has evolved in four bee families (Stenotritidae, Andrenidae, Megachilidae and Apidae). The taxonomic distribution of sting loss within the Andrenidae indicates that within this family loss of sting function has evolved upon multiple occasions. Another result of relaxed selection might be the small size of the processus medianus, the site of articulation of the furcula in bees. Hermann & Chao (1983) showed that the furcula was very important for precision in sting movement. In bees, the reduction of the processi mediani may result from a reduction in need for the precise stinging movements involved in prey paralysis which are required by the wasps. However, this does not explain either the comparatively small overall size of the furcula itself in the wasps in comparison to most of the bees or the great variation in furcula form among the bees (Fig. 11).

Loss of sting function (as a sting) has not always resulted in a decrease in size or robustness of all of the parts of the sting apparatus. For example, *Ctenocolletes* has remarkably robust 7th and 8th hemiterga (Fig. 2D) and the modification of the first rami of *Orphana* is quite remarkable (Fig. 2B). It remains to be seen whether the sting apparatus has assumed a different function in these bees. One possibility has been suggested by Houston (pers. comm.), who has found mite hypopi in the sting chambers of three species of *Ctenocolletes*. He suggests that the sting chambers of some bees might be adapted for mite transport. He further suggests that the setae on the 7th hemitergites in some taxa could be involved in this coadaptation. It would be interesting to look for mites in the sting apparatus of other bees with reduced stings. Another possible alternative function for the sting sclerites could be associated with mating processes. The retention of sensilla on the sting shaft even in species with considerably reduced stings, such as *Macrotera* (Fig. 8F), indicates that there is some functional significance for this apparatus even when it is no longer capable of penetrating flesh.

Apart from modifications associated with sting reduction (Popov, 1953; Radovic & Hurd, 1980; Michener, 1990) very little of the considerable variation in bee sting morphology has been noted previously (but see Hazeltine, 1967; Toro & Rojas, 1970;

Iuga, 1973; Toro, 1973; Aravena & Toro, 1985; Ruz, 1986, 1991; Roig-Alsina, 1989, 1990, 1991). Variation has been found at all taxonomic levels of study – among families, subfamilies and tribes (Michener, 1944; Hazeltine, 1967; this paper), and among closely related genera (Aravena & Toro, 1985). Variation is even found among closely related species: Toro (1973) and Toro & Rojas (1970) documented variation in the 7th hemitergites among species within subgenera of *Leioproctus*. A major conclusion of this study is that all future analyses of bee systematics should include treatment of the sting apparatus. Thus, descriptions of new genera and phylogenetic studies, at least at higher levels, should all include characters derived from the sting apparatus and preparations of these structures should be made as routinely as is the case with male terminalia.

Much of the variation outlined here would appear to be of great potential utility in phylogenetic studies of bees. For example, several additional characters putatively supporting bee monophyly have been discovered. For example, the loss of sensilla on the apex of the gonostyli and the reduction and reorientation of the processus medianus at the base of the sting shaft.

Five out of seven members of the Pemphredoninae used here, including two congeners to the single exemplar used by Alexander & Michener (1995; *Passaloeus cuspidatus* Smith), have divided 7th hemiterga. In all six the divided antecosta is free from the laminae spiraculari for a considerable portion of its length and each half is rotated posteriorly in comparison to the antecostae of preceding segments. They project towards one another and sometimes almost join (they do join in *Diodontus*). Nonetheless, the sclerotized connection that usually joins them is interrupted medially, at least narrowly. This finding is in contrast to the observations of Melo (1999) who states that the condition for pemphredonines is with the hemiterga 'connected anteriorly by a broad bridge' except in *Spilomena* and *Arpactophilus* which have the same character state as bees, 'two separate lateral plates, connected by membrane only.' Melo also found complete separation of the hemiterga in his three exemplars of the Spheciform tribe Ammoplanini – *Pulverro*, *Ammoplanus* and *Timberlakena*, which he moved from the Pemphredoninae to the Astatinae.

The condition found in the pemphredonines differs from that found in most bees. In bees, the divided halves of the antecosta are fused to the laminae spiraculari throughout forming part of a marginal ridge that surrounds most of each hemitergite. The crabronid *Pulverro* has exactly the same arrangement (pers. observ.). The wider range of possibly intermediate states in the wasps suggests one way in which completely separated hemitergites in bees may have

arisen. The antecosta could initially have become divided medially (as in most pemphredonines) while remaining completely separate from the laminae spiraculari. Later, the reduced portions of the antecosta could have fused to the rest of the 7th hemitergite, forming the medial portion of the marginal ridge as in *Pulverro* and most bees. Interestingly, in the Melittidae and also *Protoxaea*, *Ctenocolletes* and *Stenotritus*, the medial portion of the marginal ridge (which is the part most likely to be a remnant of the antecostal ridge) is unusually short and/or bordered by an unsclerotized region of the lamina spiracularis. Thus, the condition of the medial portion of the marginal ridge and the adjacent section of the lamina spiracularis in these bees might represent an intermediate condition between that found in apoid wasps and the other bees in which the marginal ridge is fused to the lamina spiracularis along its entire length. In this context, it is worth noting that each of these taxa (except *Stenotritus* which was not included) were found to be the sister group to the rest of the bees in at least one of the multiple phylogenies presented by Alexander & Michener (1995). However, whether any of these 7th hemitergite morphologies are indeed plesiomorphic to the bees will remain unknown pending more detailed morphological and/or molecular phylogenetic analyses of the Apoidea.

The Stenotritidae are often considered as a family with limited morphological variability (Alexander & Michener, 1995; Michener, 2000). However, their sting apparatuses are remarkably different (Fig. 2C,D). That of *Stenotritus* being one of the more weakly sclerotized among the bees and also comparatively readily flattened (as in Fig. 2C). Conversely, the sting apparatus of *Ctenocolletes* is one of the most heavily sclerotized and also the most markedly convex of all bees surveyed. The structure of the 8th hemitergites is particularly divergent between the two, being small and flat with a weakly developed apodeme in *Stenotritus* and very large, dorsally convex and with a large apodeme in *Ctenocolletes*. At least the morphology found in the exemplar of *Ctenocolletes* is representative of the genus. Houston (pers. comm.) has found little variation among the sting sclerites of an additional four species.

It remains to be seen whether the variation observed will help resolve the ambiguities in relationships among the major clades of bees indicated by Alexander & Michener's (1995) analysis. However, even a superficial inspection of the variation would seem to support the sister group relationship between the Stenotritidae and Oxaeinae within the Andrenidae suggested in some of their analyses. Although it is possible that much of the similarity I observed between these taxa stems from sting reduction (itself a character which would add support to

their close affinity), other similarities in their sting morphology are not so readily explained away as components of overall sting reduction. For example, there is no reason to expect that bees with markedly reduced stings should also have setose 7th hemiterga, nonetheless, this was found in all preparations of Oxaeinae and Stenotritidae, but among non-Andrenidae only in *Trachusa*, a genus with many other unusual modifications of the sting sclerites. Similarly, the lateral process of the 7th hemitergite is curved posteriorly forming the lateral margin of the lateral lamella only in these bees (Figs 2C, 4C).

The phylogenetic relationships of the Melittidae continue to be problematic. Alexander & Michener (1995) divided this group into three separate families based upon the results of their phylogenetic analyses. Michener (2000) treats them as one family with each of the families of Alexander & Michener (1995) given subfamily status, as in Table 1 here. No strong character from the sting apparatus would seem to provide clear and unambiguous support for the monophyly of the Melittidae. The reduction of the lamina spiracularis posteriorly near the medial portion of the marginal ridge of the 7th hemitergite may be a synapomorphy for the family; however, as noted above, this character state may well be plesiomorphic. The only other character discovered in the sting apparatus that may support a monophyletic Melittidae is the comparatively gradual narrowing of the sting shaft bulb to the stylet. This character state was observed in all members of the family except *Hesperapis* and only sporadically among other bees and in none of the wasps.

Another area in which sting morphology may provide important phylogenetic information is for the various cleptoparasitic Apidae. Roig-Alsina & Michener (1993) obtained substantially different phylogenies for the long-tongued bees when either characters related to cleptoparasitism or the cleptoparasites themselves were removed from their analyses. It remains unclear how many separate origins of cleptoparasitism there have been among the Apidae (Rozen, 2000 lists ten). However, at least four separate origins are included in the exemplars treated here, once in *Coelioxoides* which is in the apine tribe Tetrapediini, at least once in the common ancestor of the Nomadinae here represented by *Nomada* and *Epeolus*, and once each for *Osiris* and *Leiopodus*. There are certainly character states from the sting apparatus which these taxa share, presumably as convergences. These include the comparatively narrow structure of the entire sting apparatus, achieved as a result of the plates being orientated more or less in parallel and strongly dorsally directed. That this is likely to be a convergent character state in the various cleptoparasitic groups of Apidae is suggested by its also occurring in the

cleptoparasitic Megachilid genus *Coelioxys*. However, there are also character states which seem to separate some cleptoparasitic groups. For example, the long flange to the first valvifer found in *Leiopodus* presumably developed from the smaller structure found in *Epeolus*, *Nomada* and also some non-parasitic Apidae, such as *Exomalopsis*. However, there is not even a small tooth in this region in *Osiris*. There is also considerable variation in the structure of the 7th hemiterga in these taxa (Fig. 5C,F).

There are additional character states that would appear to represent strong synapomorphies for sub-taxa of bees. The ventral concavity of the second valvifer in the Nomiinae; details of the structure of the lateral process of the 7th hemitergite as a synapomorphy for the [Nomiinae + Halictinae]; the blister-like swelling on the lamina spiracularis of the 7th hemitergite of Megachilinae (all except the genus *Ochreriades*); and the dorso-ventral flattening of the ventral arms of the furcula in long-tongued bees are examples. Nonetheless, it is clear that the sclerotized parts of the sting apparatus of bees provide many useful characters for taxonomic and phylogenetic research.

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