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POSSIBLE FUNCTIONS OF THE SUB-GENITAL PLATES OF FEMALE LIBELLULID DRAGONFLIES (ANISOPTERA : LIBELLULIDAE)

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A close examination of two species and a survey of a further 281 species of libellulid dragonflies, representing 25% of the family and including members of all sub-families, has shown that the sub-genital plate is extended by more than a third of the length of the 9th sternite in 38% of the species examined (in a few it exceeds the length of sternite 9), by between a tenth and a third in 16%, and by less than a tenth in 45%. Extended plates are slotted in 39% of species and unslotted in 61%. During copulation the penis rides into the slot if one is present, but in species with extended unslotted plates, the penis is much lengthened to allow it to reach into the female's genital opening. In some species with slotted plates, a lengthening of the inner branches of the hamules allows the branches to engage with specialised recessed notches situated proximally on the plates. In species with unslotted plates, such notches are more commonly placed distally, and the hamules are not lengthened. Extended plates occur in members of 6 libellulid sub-families, and they have probably evolved several times independently. The occurrence of extended plates is most probably an adaptation for specialised modes of oviposition. The possibility that they are also significant for sperm competition or for species isolation is considered.

INTRODUCTION

Copulating males clasp females with specialised structures in many insect species. Such clasping may serve a number of possible functions : (1) it may allow a male to secure a female and prevent her escape ; (2) in predatory species it may prevent her from attempting to eat the male ; (3) it may prevent take-overs by rival males ; (4) it may enable a male to gain the purchase on the female's abdomen needed for copulation ; (5) it may play a role in mate recognition ; and (6) it may help a female to assess the fitness of a male (intersexual selection) (DARWIN, 1871 ;

THORNHILL & ALCOCK, 1983 ; EBERHARD, 1986). During copulation male libellulid dragonflies clasp females on the head with their terminal claspers and grip the sub-genital plate close to the female's genital opening with the hamules (CORBET, 1962 ; WATSON, 1966 ; MILLER, 1981).

Little is know about how the hamules lock onto the plates, nor what correlated modifications occur in males when the plates are much enlarged as is the case in many corduliids, gomphids and libellulids. There is also uncertainty about why the plates are enlarged in some species and small in others. In this paper, I describe the hamule-sub-genital plate engagement and genital modifications in two libellulid species which have enlarged plates, and then make a brief survey of the Libellulidae examining the occurrence of enlarged plates in each sub-family. The function of the plates is discussed in connection with achieving copulation, sexual selection, species isolation and oviposition. It is concluded that the plates are extended in some genera primarily as an adaptation for specialised modes of oviposition.

MATERIAL

Crocothemis sanguinolenta Burmeister (Sympetrinae) was collected at Hunter's Lodge in Kenya (MILLER, 1984) and *Urothemis edwardsi* Selys (Urothemistinae) from the Okavango swamps in Botswana. They were examined alive and also after fixation in 2% formaldehyde. Scanning electron micrographs were obtained from dried specimens, sputter-coated with gold, using a Philips PSEM 500. Copulatory positions and interactions were assessed by manipulation of the genitalia.

In addition the females of 281 other species of libellulid were examined, representing about 25% of the family (DAVIES & TOBIN, 1985 ; TSUDA, 1986). Most of these were dry specimens in the collection of the British Museum (Natural History), but some were from my own collections, and a few were from drawings of Japanese species in HAMADA & INOUE (1985). The selection was arbitrary (but not random) depending on availability and opportunity.

RESULTS

Inspection of photographs and observations in the field show that many libellulids copulate with the long axis of the female's abdomen (segments 3-8) held at about 45° (and sometimes at up to 60°) to the long axis of the male's abdomen. This position probably allows the 2nd, 3rd and 4th segments of the penis to be used in a fully straightened position (i.e. at 180° to each other). It helps to explain how mating occurs in species where females possess very long plates.

In most Libellulidae the ovipositor is much reduced. The lateral valvulae (gonapophyses) are represented by a pair of small stylets on the 9th sternite ; the median valvulae are not present in the adult, and the anterior valvulae contribute to the formation of the sub-genital plate which is sometimes paired or bears a pair of extensions (valvula vulvae, valvula laminae, or vulvar scales) (ASAHINA, 1954 ; SCUDDER, 1971 ; MATSUDA, 1976). Here I will use the term sub-genital plate to include the paired processes.

The claw on the inner branch of the hamule is believed to grip part of the sub-genital plate during copulation (WATSON, 1966). Contractions of muscle 11 (M11) close the claw, and at the same time swing the ligula posteriorly thereby driving the penis into the female's genital opening (MILLER, 1981, 1982).

UROTHEMIS EDWARDSI

In this species the sub-genital plate extends just beyond the posterior end of the 9th segment and is about 2.1 mm long. It is slotted, i.e. it contains a medial cleft 0.85 mm deep (Figs 1, 2). The region of cuticle bounding the slot is pliant, whereas other parts of the plate are well sclerotised. The posterior end of the plate bears about 14 articulated bristles on each side. At the anterior end of the plate on the inner (dorsal) surface, there is a pair of recessed and sclerotised notches (Fig. 3). The posterior margin of the 9th sternite is also slightly extended and is bent downwards.

Within the female, the sperm-storage organ consists solely of a large sac, the bursa, about 1.0 mm long, 1.2 mm wide and 0.6 mm deep. There is no spermatheca.

The uninflated 4th segment of the penis is about 1.02 mm long. When fully extended (i.e. inflated and with the 4th segment at 180° to the 2nd) it can reach through the female's genital opening to the bursa by riding into the slot in the sub-genital plate, deforming the pliable inner margins as it does so (Fig. 4). It has a dorsally situated buttress which presses against the cuticle above the female's genital opening. This probably causes the 4th segment to rotate dorsally in the female as the lateral and medial lobes enter her genital opening. The medial process consists of a sclerotised central 'pulpi' which on inflation first extends distally and then swings dorsally through 90°. It bears two long, curved and inflatable sacs, which are probably able to enter the bursa (Fig. 7). The duration of copulation in this species has not been measured.

The outer branch of the hamule is reduced, but the inner branch is straight and 1.1 mm long with a strong claw at the apex. Contraction of M11 causes each inner branch to swing laterally thereby enabling it to hook its claw into the notch on the plate.

CROTOTHEMIS SANGUINOLENTA

In the female, the sub-genital plate forms a single undivided (unslotted) structure, extending 1.95 mm from the posterior margin of the 8th segment and reaching beyond the posterior margin of segment 10 (Figs 8, 9). On the lateral posterior margin of the plate there are about 6-7 indentations on each side, lightly sclerotised in some specimens. Small articulated bristles are scattered in this region (Fig. 10).

As in the previous species, internally the female has a single large sperm-storage organ, the bursa, about 1.0 mm broad, 0.8 mm long and 0.2 mm deep, and there is no spermatheca.

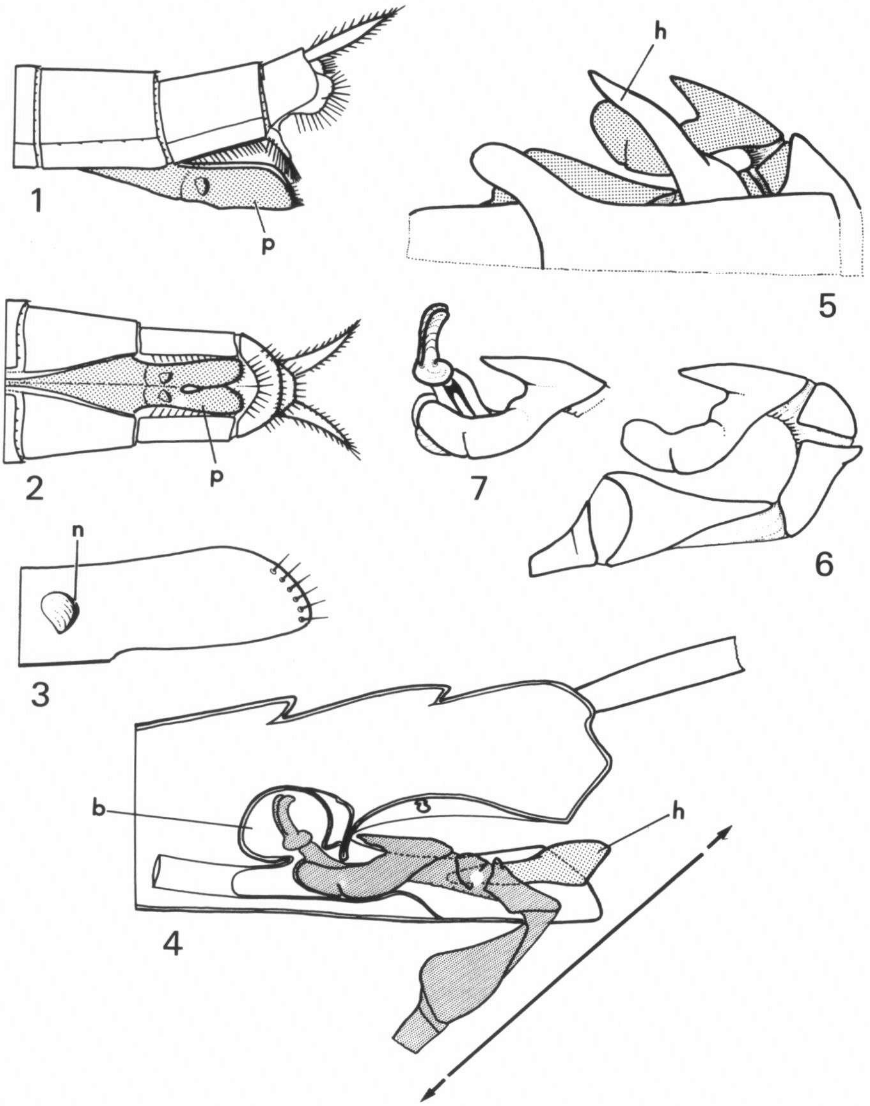

Fig. 1-7. *Urothemis edwardsi*; (1-3) terminal segments of the abdomen of a female showing the sub-genital plate (hatched): (1) ventral view (p, sub-genital plate), (2) lateral view, (3) inner (dorsal) view of the right plate showing the notch (n, notch); – (4) positions of the genitalia during copulation (male hatched), the medial lobes are shown within the bursa (b, bursa; h, hamule); – (5-7) secondary genitalia: (5) lateral view (h, hamule), (6) penis uninflated, (7) 4th segment of penis inflated.

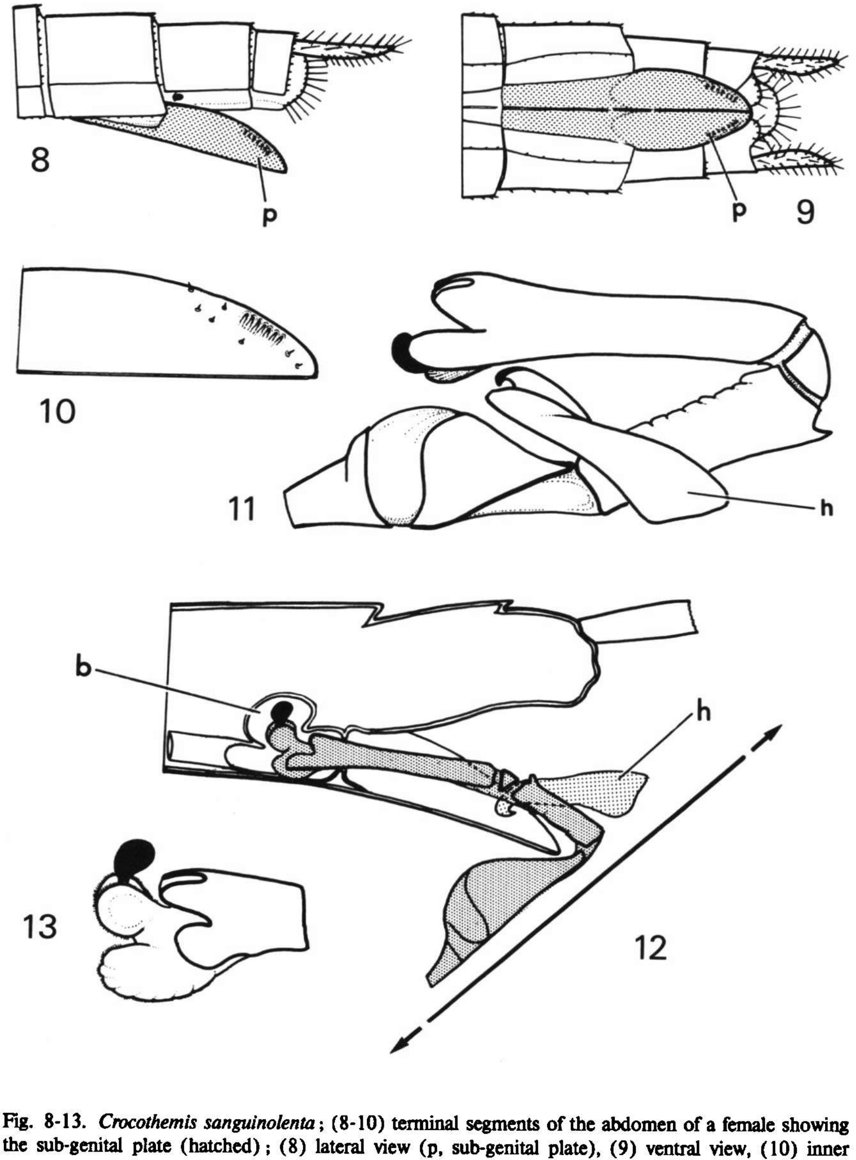

Fig. 8-13. *Crocothemis sanguinolenta*; (8-10) terminal segments of the abdomen of a female showing the sub-genital plate (hatched); (8) lateral view (p, sub-genital plate), (9) ventral view, (10) inner (dorsal) view of the right half of the plate showing the seven small notches; – (12) positions of the genitalia (male hatched) during copulation (b, bursa); – (11, 13) secondary genitalia: (11) penis uninflated (h, hamule), (13) 4th segment of penis inflated.

The 4th segment of the penis bears a pair of small sclerotised lateral lobes (Fig. 11), a bristly inflatable apical lobe and a medial complex comprising a single hammer-like and sclerotised cornu, together with a pair of very bristly sacs. On inflation the medial complex protrudes and swings dorsally while the apical and medial lobes inflate (Fig. 13) (cf. SIVA-JOTHY, 1984). The short hamules are well placed to grip the lateral posterior margins of the plate where the rows of indentations occur. The uninflated 4th segment of the penis is 2.1 mm long while the length of the straightened 2nd, 3rd and 4th segments together is 3.2 mm. In the female, the distance from the distal tip of the plate to the opening into the bursa is about 3.4 mm and with full inflation the straightened penis can therefore probably reach into the bursa (Fig. 12). Copulation usually takes place on the wing, and, as in *C. erythraea* (SIVA-JOTHY, 1984), it is very brief, lasting a mean of 9.8 s (s.d. ± 2.8 s ; n = 16).

SURVEY OF LIBELLULID SPECIES

The females of altogether 283 species in 97 genera have been examined, representing 25% of the family (1118 spp.) and including members of all 11 sub-families (although only one onychothemistine species has been seen) (DAVIES & TOBIN, 1985 ; TSUDA, 1986).

Because my main focus of interest is in the sub-genital plates, the species have been divided into 3 classes according to the length of the plate : – **Class I** : species in which the sub-genital plate is either not extended posteriorly, or is extended for less than 10% of the length of sternite 9. – **Class II** : species with sub-genital plates extending for between 10 and 33% of the length of sternite 9. – **Class III** : species with sub-genital plates extending for more than 33% of the length of sternite 9.

Table I

Number of species surveyed in each sub-family according to the size of the sub-genital plate

Sub-families	Class I	Class II	Class III	Total N° of species in sub-family	Percentage surveyed
Tetrathemistinae	15	1	5	90	23
Brachydiplacinae	6	4	21	123	25
Leucorrhiniinae	3	6	1	36	28
Libellulinae	51	1	0	274	19
Sympetrinae	14	24	47	230	37
Trithemistinae	28	1	1	154	19
Onychothemistinae	1	0	0	8	13
Palpopleurinae	3	2	8	33	39
Trameinae	4	7	15	109	24
Urothemistinae	0	0	11	23	48
Zygonychinae	3	0	0	38	8
Total	128 (45%)	46 (16%)	109 (38%)	1118	25

The distribution of examined species in the different sub-families is shown in Table I.

In those genera in which 3 or more species were examined, 13 genera (50%) had all their species in one class, 11 (42%) had them in two classes, and 2 (8%) in all three classes.

In the Libellulinae, Trithemistinae, Onychothemistinae and Zygonychinae, 97% of the species examined belong to Class I. In the Urothemistinae 100% belong to Class III. However, the sub-families Tetrathemistinae, Brachydiplacinae, Leucorrhiniinae, Sympetrinae, Palpopleurinae and Trameinae have some species in each of the three classes, although, except for the Tetrathemistinae, most of their species (> 70%) are in classes II or III. Thus, in these 6 sub-families, extended sub-genital plates are very common, whereas in the remaining sub-families they are less common. These facts suggest that increased plate size has been selected for several times independently (polyphyletically).

Amongst class III species, 42 (39%) have slotted (or cleft) plates and 66 species (61%) have unslotted plates. Species were counted as being slotted only when the plate was cleft for more than a quarter of its length. In 23 genera all the class III species within a genus were either slotted or unslotted. Only 3 class III genera (*Sympetrum, Urothemis* and *Aethriamanta*) contained a mixture of slotted and unslotted species. Closely related species, therefore, tend to be uniform with regard to slotting.

The sub-genital plates were found to be at least partly turned ventrally in a total of 30 species (11%), all occurring in one of 3 sub-families (3 in Brachydiplacinae, 4 in Palpopleurinae and 23 in Sympetrinae). In 19 of these, the dorsal face of the plate is turned through about 90°, pointing downwards, whereas in 11 species it is bent down by a smaller amount.

Table II

Sub-genital plate size in some selected genera.
The number of species in each plate-class is shown
(u = unslotted plate ; s = slotted plate)

Genera	Class I	Class II	Class III
Libellulinae			
Orthetrum	13	0	0
Sympetrinae			
Bradinopyga	1	0	2 (all u)
Erythemis	1	1	5 (all u)
Neurothemis	0	1	10 (all u)
Sympetrum	12	11	14 (6u ; 8s)
Trameinae			
Tramea	0	0	12 (all s)
Urothemistinae			
Aethriamanta	0	0	3 (2u ; 1s)
Urothemis	0	0	6 (4u ; 2s)

The distribution of classes in a few selected genera is shown in Table II. Within *Sympetrum* there are approximately equal numbers of species in all 3 classes, with, in class III, 43% being unslotted and 57% slotted. Likewise, *Urothemis* and *Aethriamanta* both contain some species with deeply slotted plates and others with unslotted plates, as already mentioned. *Orthetrum* spp. are typical of other libellulines in not having extended plates, whereas all *Tramea* spp. examined have deeply slotted and much enlarged plates.

DISCUSSION

COPULATION

In *C. sanguinolenta* the female has an exceptionally long and unslotted sub-genital plate, and copulation is made possible by the considerably lengthened second and fourth segments of the penis. The hamules, which are not enlarged, probably grip the plate distally where several notches occur. The females of all *Crocothemis* spp. examined have plates which are unslotted and to some degree extended. *C. divisa* resembles *C. sanguinolenta* although the plate is smaller, whereas *C. erythraea, C. nigrifrons,* and *C. servilia* have plates which are smaller and downwardly turned, and the males of these species have penes only moderately lengthened. In *C. erythraea* the plate bears a single pair of notches 0.78 mm from the tip and the inner claw of the male's hamule is of a corresponding length.

In contrast, the long sub-genital plate of *U. edwardsi* is deeply slotted, and the penis, which is not greatly lengthened, must ride into the slot to reach the genital opening of the female. The plate bears a pair of proximal notches into which the long and straight inner hamule branches may be able to hook. Five other *Urothemis* spp. were examined: *U. assignata* and *U. luciana* were found to resemble *U. edwardsi,* whereas *U. abbotti, U. aliena* and *U. signata* have similarly large but unslotted plates.

Thus, in species in which the females have evolved enlarged slotted plates there need be little modification of the male's penis, whereas in those with extended but unslotted plates, the penis is much lengthened.

SURVEY OF LIBELLULID SPECIES

The survey has shown that in different species the sub-genital plates vary greatly in shape whether they are extended or not: they may be slotted, cleft, or widely divergent at the posterior end, as well as being sometimes strongly turned downwards. Of the 283 species examined, 38% have sub-genital plates more than a third as long as sternite 9 (class III), 16% have plates 10-33% as long (class II), while the remaining 45% have plates which extend little or not at all beyond the posterior margin of segment 8 (class I). Extended plates are common in 6 libellulid subfamilies and uncommon in 4: they are common also among corduliids and gomphids. They have apparently been modified by selection many times independently, presumably evolving from ancestors with small plates.

No extensive survey of corresponding male structures has been made, but in several species females with large unslotted plates were found to be matched by males with very long penes as in *C. sanguinolenta* (e.g. *Aethriamanta brevipennis, Bradinopyga cornuta, Hemistigma albipuncta, Crocothemis divisa, Uracis fastigiata, U. infumata*), while females with large but slotted plates were matched by males with enlongated hamules but with penes more normal in size, as in *U. edwardsi* (e.g. all 12 spp. of *Tramea*, and in *Aethriamanta rezia, Urothemis luciana, Hydrobasileus brevistylus, Tyriobapta bispina* and *Sympetrum eroticum*). In these species, therefore, extended, unslotted plates are correlated with lengthened penes, whereas slotted plates are correlated with modified hamules.

In species with the plate turned ventrally and not extending posteriorly, no modification of the male genitalia or copulatory position has been found. In the few species with extremely long unslotted plates, extending well beyond the end of the abdomen (*Uracis fastigiata, U. imbuta, U. infumata, U. ovipositrix, Sympetrum cordulegaster* and *S. parvulum*), copulation may be achieved either with the plate passed to one side of the male (S. W. DUNKLE, pers. comm.), or bent downwards.

POSSIBLE FUNCTIONS OF THE PLATES

In all species, the plate is presumed to be gripped by the male's hamules thereby allowing the male to gain a purchase on the female and to drive the penis through the vagina. Together with the claspers on the head, the hamule-plate lock may also help to prevent a rival male from taking over the female during copulation. These may be the original and most important functions of sub-genital plates and hamules.

In addition, they may be important for species isolation (TENNESSEN, 1982). In many insects, recognition is thought to occur before genital contact is made, using visual, chemical or auditory cues (THORNHILL & ALCOCK, 1983 ; WEST-EBERHARD, 1984 ; EBERHARD, 1986). Visual features, such as body and wing colour and patterning, and species-specific behaviour (CORBET, 1962 ; WAAGE, 1975, 1979 ; UBUKATA, 1983 ; FRANTSEVICH & MOKRUSHOV, 1984) probably provide important clues about species identity in most dragonflies before the tandem is formed. However, male libellulids typically approach and seize females very rapidly at the water and additional isolating mechanisms may be called for.

In some families, the males' terminal claspers vary greatly in shape between species, as indicated by their usefulness to taxonomists. They may be important in species isolation acting either mechanically (DUFOUR, 1844) or through the excitation of particular groups of tactile receptors on the female (LOIBL, 1958 ; PAULSON, 1974 ; TENNESSEN, 1982 ; ROBERTSON & PATERSON, 1982). In libellulids, however, the claspers are not commonly used in taxonomy and their shape varies less between species than in some other families. If the claspers are not involved, mate discrimination may depend on other mechanisms such as the hamule-plate lock, acting mechanically or through sensilla. Both hamule and plate shape sometimes show much intrageneric variation and they have been much used by taxonomists to distinguish gomphid, corduliid and libellulid species (e.g. NEEDHAM & WESTFALL, 1954; CONCI & NIELSEN, 1956; ROBERT, 1963; CANNINGS & STUART, 1977; GEIJSKES & VAN TOL, 1983). Even when the plates are small (class I) they, together with the hamules, may still be highly variable, e.g. in *Orthetrum* and *Trithemis* spp. (PINHEY, 1961; cf. EBERHARD, 1986). They could, therefore, form mating barriers between sympatric species (WATSON, 1966). Plate enlargement, however, is unlikely to arise as a means of preventing cross-species mating, and another explanation for enlargement is called for.

One possibility is that extended plates play a role in sperm competition. Unslotted and lengthened plates may prevent a male from reaching into all parts of a female's sperm-storage organs with the penis, from where rivals' sperm could be removed. Males in turn may have responded by a lengthening of the penis. Alternatively, penis lengthening may have initiated retaliatory extensions of the sub-genital plate.

Various types of intersexual competition, consequent on the differing interests of males and females, have many times been postulated (DAWKINS, 1982). In the females of a few libellulid species, some features of the internal genital anatomy have been thought to prevent males from removing all the sperm from the storage organs (MILLER, 1982) (see EBERHARD, 1986, and SIVA-JOTHY, 1987b). In *Calopteryx maculata* most or all of the rival sperm is commonly removed from females during copulation (WAAGE, 1979, 1984), but at least in some libellulids only a proportion of the stored sperm is normally removed (MCVEY & SMITTLE, 1984; WAAGE, 1986; but see SIVA-JOTHY, 1987a). However, if mechanisms have evolved to prevent total removal, they are more likely to have made use of internal modifications since they will be simpler and more effective. Sperm competition is, therefore, unlikely to account for the extension of the plates.

A more plausible explanation for the development of extended sub-genital plates is that, having evolved from the endophytic ovipositor of a non-libellulid ancestor (ASAHINA, 1954; MATSUDA, 1976), they have subsequently been selected to promote a specialised mode of epi- or exophytic oviposition.

Table III indicates the types of oviposition which occur in several *Sympetrum* spp. (EDA, 1975, 1979), together with the plate-class to which each belongs. Oviposition behaviour is known to be variable within a species in several libellulids (e.g. PAULSON, 1969) and both reproductive behaviour generally (SAKAGAMI *et al.*, 1974), and oviposition behaviour in particular, vary greatly within and between *Sympetrum* spp. Table III suggests that the long plates of class-III female *Sympetrum* spp. are commonly used to push eggs into mud, whereas class-I females with short plates normally lay by dipping at the water surface, or by dropping eggs from the air (cf. EDA, 1981; ARAI, 1981).

Table III

Oviposition behaviour and the plate class of some *Sympetrum* spp.
(Data on oviposition from EDA, 1975, 1979 and pers. obs.)
(+++ = normal ; ++ = frequently ; + = seldom)

Species	Class		Oviposition	
		into mud	into water	in air
baccha	III	++	++	
croceolum	III		+++	
danae	III	+++	++	+
kunckeli	III		+++	
eroticum	III	+++	+	
parvulum	III	++	++	
pedemontanum	II			+++
striolatum	II		++	++
uniforme	II		+++	
darwinianum	I		+	+++
depressiusculum	I		+++	
flaveolum	I		+	+++
frequens	I	+++	++	
gracile	I		+++	
infuscatum	I			+++
maculatum	I			+++
risi	I			+++
sanguineum	I			+++

Ventrally turned plates may also be used by epiphytic ovipositors to press eggs down onto the substrate (plants, mud, stones, etc.). Such plates occur in a number of corduliid species as well as in many sympetrine libellulids (e.g. 3 *Crocothemis* spp. ; 3 *Erythemis* spp. ; 6 *Erythrodiplax* spp. ; 5 *Neurothemis* spp. and 6 *Sympetrum* spp.).

In some class III species, however, which have ventrally turned plates (e.g. *Nannophya pygmaea* and *Crocothemis erythraea*) and in others with posteriorly extended plates, (e.g. *C. sanguinolenta, U. edwardsi* and *Tramea basilaris*) oviposition is by the usual libellulid method of dipping the abdomen at the water surface (YAMAMOTO, 1968 ; SIVA-JOTHY, 1987 ; pers. obs.), sometimes with the 9th and 10th abdominal segments flexed dorsally by nearly 90° (also seen by ROBERT, 1958 in the corduliid *Somatochlora metallica*, see also STORCH *in* GEIJKSKES & VAN TOL, 1983). Extended plates are not, therefore, always associated with epiphytic or substrate oviposition, although the range of oviposition modes of which some species are capable is not known.

Extended plates may assist oviposition in another way by temporarily holding the accumulating eggs of a batch as they leave the genital opening between successive dips to the water surface, as occurs, for example, in *Sympetrum vulgatum* (class III) (ROBERT, 1958). *Tramea basilaris* and *T. limbata* sometimes dip at intervals of ca 1 min., perhaps accumulating a large batch of eggs between dips.

The extremely extended plates of *Uracis fastigiata, U. imbuta, U. infumata, U. ovipositrix, Sympetrum cordulegaster,* and *S. parvulum,* (extending 3 mm beyond the tip of the abdomen in *U. ovipositrix*), are probably used to thrust eggs into the mud at the bottom of streams (S. W. Dunkle, pers. comm.) either by bending the abdomen forwards, or possibly by flying backwards as in *Cordulegaster.*

Other modifications of the posterior abdominal segments may also assist oviposition. For example, the bilateral ventrally projecting foliations on the 8th tergite of many libelluline females probably help to scoop up a drop of water and flick it together with a batch of eggs towards or onto the bank, a type of oviposition witnessed in *Hadrothemis coacta, Potamarcha congener, Orthetrum chrysostigma, O. coerulescens, O. pruinosum, Nesciothemis farinosa* (Corbet, 1962 ; Miller, 1984, pers. obs.), *Belonia croceipennis* (Williams, 1977) and *Orthetrum triangulare* (Sugimura, 1981), all of which possess such modifications. In the survey, they were found in 4 species of Tetrathemistinae and in 23 spp. of Libellulinae (Figs 14-16), all of which belong to class I. An extended sub-genital plate might interfere with this type of oviposition, and scooping seems to be a speciality of the Libellulinae, a sub-family in which all the species examined have class I plates.

In conclusion, the sub-genital plates, together with the hamules, are probably necessary in all libellulids to allow the genitalia to engage. They may also provide for species isolation although direct evidence is lacking. Plate extensions have probably been selected for in species with specialised epi- and exophytic modes of oviposition.

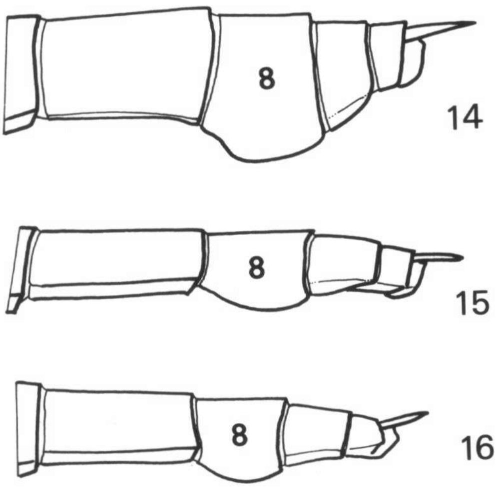

Fig. 14-16. Lateral view of the terminal segments of the abdomens of: (14) *Hadrothemis coacta,* (15) *Orthetrum brachiale,* (16) *Nesciothemis farinosa.*

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