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DESCRIPTIONS OF TWO NEW SPECIES OF THE GENUS *OLIGOAESCHNA* FROM NORTHERN TAIWAN, WITH NOTES ON THE STATUS OF THE *PRYERI*-GROUP (ANISOPTERA: AESHNIDAE)

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2 syntopic new sp. of the *pryeri*-group *Oligoaeschna*, *O. lieni* sp. n. (holotype ♂: Tsaopi bog, 850m, Yuanshan, Ilan county, northern Taiwan, 11-V-1997) and *O. tsaopiensis* sp. n. (holotype ♂: Tsaopi bog, 850m, Yuanshan, Ilan county, northern Taiwan, 11-V-1997) collected from northern Taiwan are named, described and diagnosed. Relationship amongst the members of eastern Asian *pryeri*-group is discussed and inferred mainly from their male penile structure. With regard to male penile glans structure, the *pryeri*- group is considered to be the extant sister-group of the nearctic genus *Gomphaeschna*.

INTRODUCTION

The traditional genus *Oligoaeschna* Selys, 1889 is composed of a group of primitive aeshnids confined to the Indo-Chinese and Indo-Malayan subregions of the Oriental region, with one species, *O. pryeri* Martin, having invaded northwards to Japan and another species, *O. venatrix* (Förster) east to Celebes. In LIEFTINCK's (1968) comprehensive revision, the genus was tentatively divided into two species-groups, viz. *pryeri*-group and *poeciloptera*-group, based on many morphological dissimilarities. LIEFTINCK (1968) noted that: "With a better knowledge of the last-mentioned species group [*pryeri*-group] it may ultimately prove possible and more convenient to split up *Oligoaeschna* in two subgenera, when characters are amplified from other organs." However, except H. Karube (pers. comm.), who is now making an attempt to revise the genus, the other authors (ASAHINA, 1986a, 1986b, 1990; CHHOTANI et al., 1983; ISHIDA, 1972; KARUBE, 1997, 1998a, 1998b) involved in the taxonomic work of this genus, although generally following

Lieftinck's opinion and attributing their new species to one or other of the two species groups, have not tried to develop other differential characters to separate the two groups in order to put Lieftinck's suggestion a further step ahead and make the taxonomy of this heterogeneous genus clear and natural.

In fact, it is easy to find out marked differences in the configuration of male penile glans (the apical or fourth segment of "vesicula spermalis") between the representatives of *pryeri-* and *poeciloptera*-groups in *Oligoaeschna* when we compare the KARUBE's (1998a, 1998b) figures of *O. speciosa* Karube and *O. niisatoi* Karube [*pryeri-* group] with SCHMIDT's (1915) figure of *O. foliacea* Lieftinck [*poeciloptera*-group (originally as *Jagoria modiglianii*, nec Selys; cf. LIEFTINCK 1968)]. Close inspection of this organ in five species of eastern Asian (Japan and Taiwan) *pryeri*-group *Oligoaeschna*, including the two new species described here, revealed that the *pryeri*-group *Oligoaeschna* are not as closely related to its traditional sister group as considered before, but more approach to the North American genus *Gomphaeschna* Selys, 1871.The details of this point will be elucidated later before the discussion. Terminology of venation and abdominal maculation used generally follow RIEK & KUKALOVÁ-PECK (1984) and WALKER (1912), respectively.

OLIGOAESCHNA LIENI SP. NOV.

Figures 1-6, 14, 19c

Material. – All collected by W.C. Yeh from Tsaopi bog (alt. 850 m), Yuanshan, Ilan county, northern Taiwan. **Holotype:**♂, 11-V-1997; – **Paratypes:** 1♂, 3-V-1997; 8♂, 3-V-1997; 4 ♂, 11-V-1997. Holotype will be deposited at Taiwan Forestry Research Institute (TFRI), paratypes in coll. W. C. Yeh. – Additional material: 2♂, Shenmihu lake (alt. 1100 m), Nanao, Ilan county, northern Taiwan, 4-VII-1996, L. J. Wang leg; 3 ♀ (teneral), same locality with the type series, 5-IV-1998, W.C. Yeh leg. All in coll. W. C. Yeh.

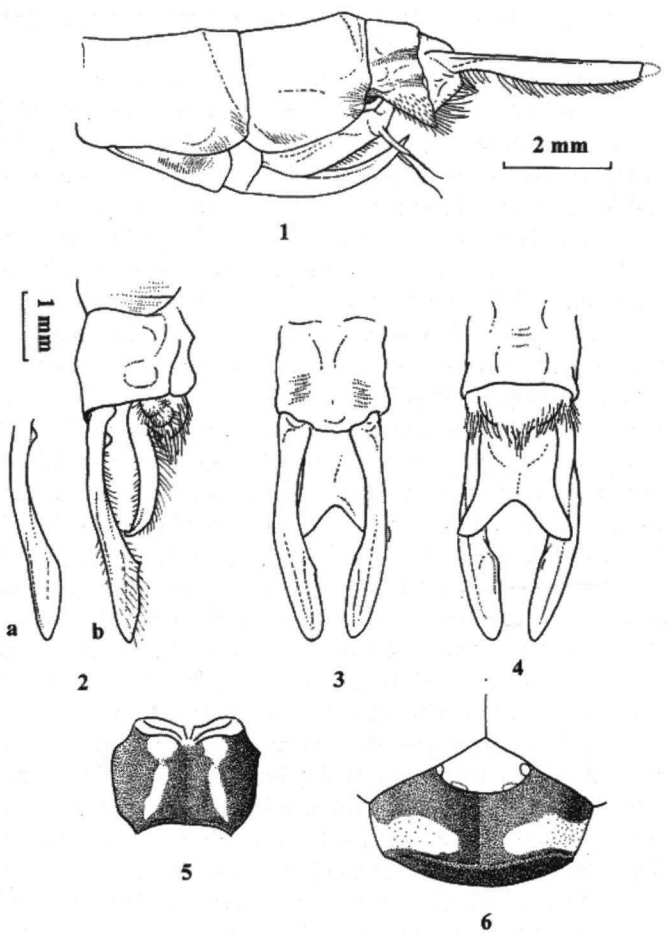
Etymology. – The new species is named after Dr. JIH- CHING LIEN for the continuous guidance and encouragement rendered to the senior author during his course of studying dragonflies.

DIAGNOSIS. – *O. lieni* differs from the other known eastern Asian *pryeri*-group *Oligoaeschna* as follows: lower margin of yellow postclypeus lacking broad dark band; male cerci are slender with shallow and broad ventral emargination and weakly apical expansion; spines of anterior lamina poorly developed with blunt apex; female cerci are longer than 9th + 10th abdominal segments.

MALE **(holotype).** – Head. – labium yellow, lateral lobes dark brown. Face generally black, base of mandible yellow; labrum laterally with a pair of transverse yellow spots. Anteclypeus dark brown; postclypeus yellow, lower margin narrowly dark brown. Antefrons yellow, black and wrinkled on upper 4/6, upper margin straight and weakly ridged. Dorsal side of frons black and shallowly concave medially, laterally invaded by a pair of transverse yellow spots and forming a T-

mark (Fig. 6); the yellow spots connected below with yellow area of antefrons. Vertex, antenna and occiput black; vertex about 1/3 width of frons, tumid, with a pair of small transverse yellow spots at top. Median ocellus deeply submerged below vertex, being obsured dorsally and invisible. Occiput black, small and a little elevated. Compound eyes pale green in living condition; interorbital suture short, a little shorter than the width of vertex. Black hairs scattered on entire area of face and head, except on the wrinkled part of antefrons; hairs longer and more densely present on dorsal side of frons, vertex and occiput.

T h o r a x. – Prothorax black, a pair of small yellow spots present at lateral margins



Figs 1-6. *O. lieni* sp. n., 1 & 2a paratypes, 2b- 6 holotype: (1) female cerci, lateral view; – (2 & 3) male cerci, lateral and dorsal view; – (4) male epiproct, ventral view; – (5) dorsal stripes of synthorax, front; – (6) T-mark on dorsal side of frons.

of middle lobe. Pterothorax black, with yellow or apple-green markings, densely covered with long brown hairs on dorsal side and less so on lateral sides. Dorsal stripes spindle-shaped (Fig. 5) and directed outward and downward toward outer ends of collar carina; lower ends attenuate and reaching almost to collar carina, upper ends connected above with a pair of round spots. Stripes of mesepimeron round at upper ends, broader and approaching humeral suture more closely in the lower half. Metepisternum with a pair of tiny spots, lower one situated at about middle point of distance from upper one to metathoracic spiracle. Metepimeron yellow at posterior 3/4. Mesinfraepisternum yellow, metinfraepisternum with a triangular spot at lower margin. Legs black, outer side of fore and hind coxae have a tiny yellow spot; apex of hind femur reaching to posterior margin of 1st abdominal segment.

Wings. – Hyaline, slightly tinged with amber at basal extremity; veins black. Pterostigma reddish-brown, braced in all wings and underlaid by 1.5-2.5 cells. Venation simple; IR1 originated at level a little distal to pterostigmal brace. RP2 markedly curved forward, especially in fore wings, proximal to the level of inner margin of pterostigma, and separated from IR2 by two rows of cells at least at apical 1/3. Rspl and Mspl straight, separated from IR2 and MA, respectively, by one row of cells. Nodal index 7: 15: 16: 18 in forewings, 9: 11: 9: 7 in hindwings; 1 cubito-anal crossvein in all wings. Triangle a little longer in forewings than in hindwings and three-celled. Hypertriangle and subtriangle uncrossed. Anal loop compact and five-celled; anal triangle three-celled. Tornus roundly angulate; membranula well developed and pale brownish.

A b d o m e n. – Black with yellow or apple-green maculation (Fig. 14b). S1 and S2 swollen, as broad as pterothorax; S3 moderately constricted at middle. Abdomen spindle-shaped from distal half of S3 to S7 and a little expanded again from distal half of S9 to S10, widest on S4 & S5 and parallel-sided on S8 & S10; S10 very short, about half length of S9. Dorsally, S2 has a pentagonal AD spot, a pair of transverse MD spots and triangular PD spots; S3-S6 have pairing sub-triangular PD spots, about equal-sized on S3-S5, smaller on S6. Laterally, S1 has a large yellow patch; S2 has large AML and PL spots, the former covering auricle (Fig. 14a); base of S3 has triangular AL spot; S4-S6 have obscure ML spot. Ventrally, bases of S4-S6 have a pair of sub-rectangular spots. Auricles well developed and semicircular in shape, protruding posteriad and armed with numerous dark denticles on posterior margin. Middorsal carina weakly present on S4-S7. Male cerci about two times as long as S10, slender, with apical 1/3 weakly expanded and apex blunt (Fig. 3); lateral view of cerci a little convex dorsally and basal 7/10 shallowly emarginate ventrally, with a basal teeth and a tiny subapical denticle at base of apical expansion (Fig. 2b). Epiproct 5/9 as long as cerci, deeply divaricate at apex with two forks markedly diverging outward (Fig. 4); depth of divarication about 1/4 length of epiproct. Apex of epiproct curved upward.

FEMALE **(paratype)**. – External morphology is generally the same as that of the

holotype, the noted variations are as follows: dorsal stripes of pterothorax unconnected with spots above it and attenuate at both ends. Wings tinged with amber proximal to Ax1 and very slightly and evenly smoked with pale brown at costal side proximal to nodus [in teneral specimens, all wings are more heavily smoked with pale brown at costal 1/2 and area proximal to apex of triangle]. Anal triangle three-celled in left wings, four-celled in right wings. Abdomen not expanded on S9 & S10; S2 with AD spot longer and MD spots smaller and dot-like, a short stripe present between MD and PD spots; lateral side of S2 yellow at lower half. Ventral sub-rectangular spots present only on S4 & S5; lower margin of S9 yellow at posterior half. Female cerci longer than S9 + S10, slender and blade-shaped, with blunt apex (Fig. 1). Ovipositor reddish-brown and reaching to posterior margin of S10; denticulate plate of S10 protruding postero-ventrad and ventrally armed with numerous closely-set and pointed spinules.

VARIATION IN MALE PARATYPES. – Paired spots on lateral sides of labrum somewhat variable, well developed as in holotype or obscure. Dorsal stripes of pterothorax generally connected with spots above it, but unconnected in two specimens; a tiny spot can be traced between MD and PD spots of S2 in two specimens. Origin of IR1 variable, at, proximal or distal to pterostigmal brace even in same specimen. Nodal index 7-10: 15-19: 15-18: 7-9 in forewings, 7-11: 9-13: 9-12: 7-10 in hindwings. Triangles generally three-celled, but two-celled in hindwings of one paratype (in the two teneral females listed in additional material, triangles are two--celled in hindwings and right forewing of one female, and three-celled in forewings). Anal loop with 3, 4 or 5 cells (2: 8: 10, N= 20). Subapical denticle of male cerci variable, obsolete in three specimens (Fig. 2a).

Measurements (mm). – holotype♂: abd. + cerci 45, hindwing 37, pterostigma 2.6; paratypes: ♀: abd. + cerci (broken at apex) 40, hindwing 34, pterostigma of forewing 2.7 and hindwing 2.8; ♂, abd. + cerci 42- 45, hindwing 35- 37, pterostigma of forewing 2.3-2.8 and hindwing 2.5-3.0.

REMARKS. – The known habitats of *O. lieni* are sphagnum bog and natural lake surrounded nearby with evergreen forests in mountainous areas, covering 850-1100m in altitude. In the type locality (Tsaopi bog), the emergence of the last instar larvae began at the end of March, and may last until the early May with only very few individuals recorded in the latter period. During this time, last instar larvae and exuviae were found clinging to the reeds (*Msicanthus floridulus*) or sedges (*Scirpus triangulatus*), which dominated the marginal herbaceous plant community of the bog. Mature adults were active from May to July. Males patrolled diurnally on small areas and protected this territory against other males, often hovering low, generally not higher than 2 meters above the ground, and turning to a different direction every half to one minute. When an intruder crossed above or nearby, the owner of the territory flew off its land to chase the intruder for a short distance, and then returned to the original site. In May, females were found to oviposit solitarily, or rarely in tandem with male, on wet and soft soil covered or uncovered with fallen leaves. The oviposition sites are generally located at the margin of bog bordered with woods in semi- shaded condition. The supposed young larvae were

collected in the same month from small shallow water depressions in these sites, and found to cling to the underside of decayed leaves accumulated at the bottom. Similar larval habitat has also been reported by TAKETO (1959) for *O. pryeri*. When disturbed, the larvae may perform feigned behavior, a common reaction also found in some of other aeshnid larvae, and with their camouflaged shape and coloration simulating the surrounding decayed detritus, the presence of larvae is somewhat difficult to recognize.

OLIGOAESCHNA TSAOPIENSIS SP. NOV.

Figures 7-12, 13, 18, 19f

Materials. – **Holotype** ♂: Tsaopi bog (alt. 850 m), Yuanshan, Ilan county, northern Taiwan, 11-V-1997; – **Paratypes** 2♂, same locality, 18-VI-1996; 1♂, same data with the holotype; all collected by W. C. Yeh. Holotype will be deposited with Taiwan Forestry Research Institute (TFRI), paratypes in coll. W. C. Yeh.

Etymology. – The specific name is derived from the type locality "Tsaopi" bog.

DIAGNOSIS. – *O. tsaopiensis* differs from the other known eastern Asian *pryeri*-group *Oligoaeschna* as follows: slender and stick-shaped dorsal stripes present on pterothorax; males have unique razor knife-shaped cerci and proportionately longer epiproct with shallow apical emargination; the spines of anterior lamina is strongly developed and robust; RP2 generally separated from IR2 by one row of cells.

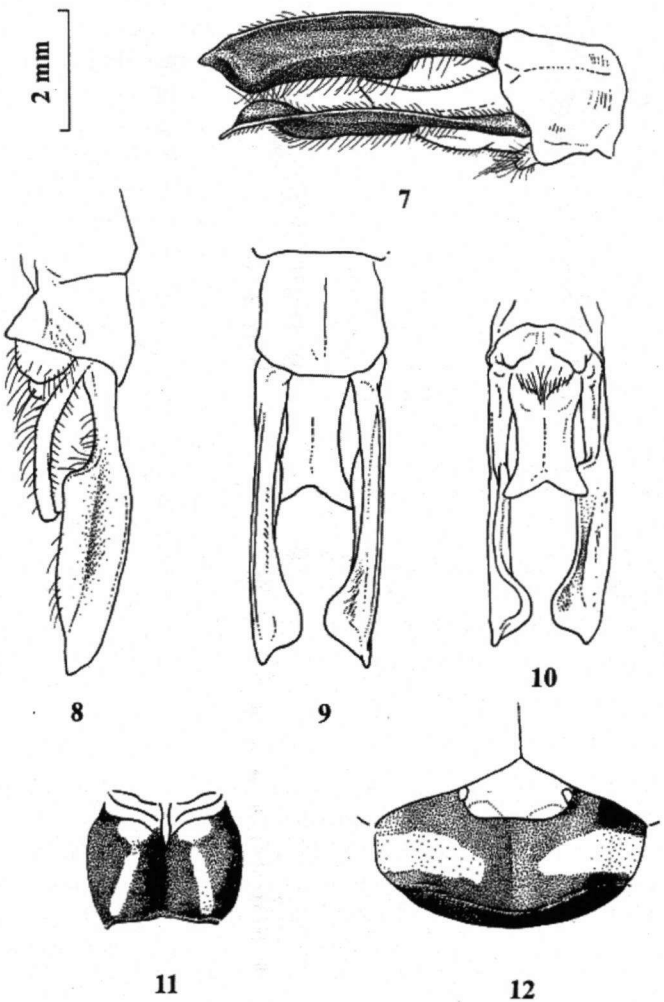
MALE **(holotype)**. – Head: colour pattern and structure of head similar to *O. lieni*, but compound eyes are more expanded. Labrum and anteclypeus black, lower margin of postclypeus bordering anteclypeus broadly black, with a pair of small protuberances of same colour protruding into yellow area at near lateral ends. Antefrons black and wrinkled at upper 5/6. Paired yellow spots of vertex round, larger and more conspicuous than in *O. lieni*, about same size as median ocellus; upper margin of frons more weakly ridged. T-mark on dorsal side of frons with anterior bar thicker and preocular bar thinner (Fig. 12). Compound eyes pale green in living condition, markedly expanded laterally.

Thorax. – Prothorax black with a tiny spot at lateral margin of middle lobe. Dorsal stripes of pterothorax slender, stick-shaped and not tapering at both ends; upper ends of dorsal stripes very close to or a little connected with spots above it (Fig. 11), the spots more transversely elongate than those of *O. lieni*. Lateral sides of pterothorax with similar markings as in *O. lieni*, however, upper spot on metepisternum is larger, and lower spot replaced by a tiny slim stripe; an inconspicuous tiny spot present below metathoracic spiracle. Legs black, outer sides of fore coxae yellow; middle and hind coxae specked with tiny yellow spots at outer sides.

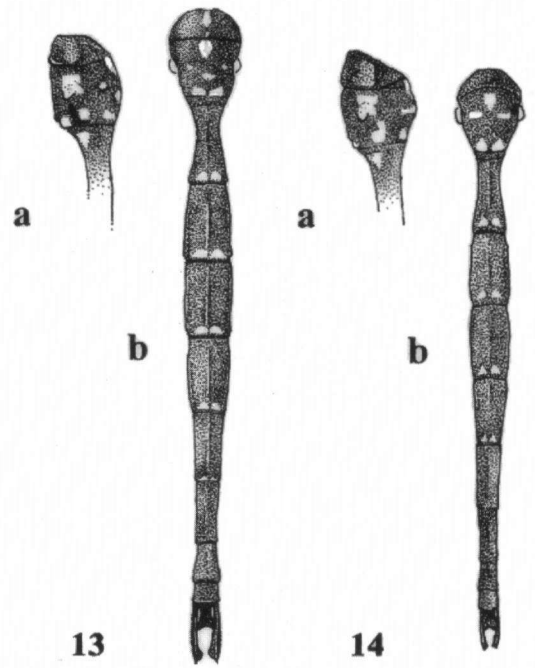
Wings. – General venational characters similar to those of *O. lieni*. The differences noted are as follows: Pterostigma dark brown, longer and underlaid by 2.5-3.0 cells; RP2 separated from IR2 by single row of cells except for apical 4 or 5 double

cells. Nodal index 7: 16: 16: 7 in forewings, 8: 11: 11: 10 in hindwings; anal loop four-celled in left wing and five-celled in right wing.

A b d o m e n. – Shape of abdomen similar to that of *O. lieni*, but paired PD spots on S3-S6 are more round in shape and closely approaching each other. Maculation of abdomen is as follows: dorsally, S1 has an elongate AD spot and small PD spot; S2 has a spearhead-shaped AD spot, a pair of dot-like MD spots, a pair of closely set sub-oval PD spots and an irregular-shaped spot between MD and



Figs 7-12. *O. tsaopiensis* sp. n., holotype: (7-9) male cerci, oblique, lateral and dorsal view; – (10) male epiproct, ventral view; – (11) dorsal stripe of synthorax, front; – (12) T-mark on dorsal side of frons.



Figs 13 & 14. Abdominal maculation of *O. tsaopiensis* sp. n. (13) and *O. lieni* sp. n. (14): (a) lateral side of S2; – (b) dorsal view.

PD spots; paired semi-oval PD spots present on S3-S7, tiny and inconspicuous on S7 (Fig. 13b). Laterally, a yellow patch faintly present on S1; S2 with a large AML spot covering auricle, a PL spot and a spot about same size as PL spot at postero-lower corner (Fig. 13a); S3 has a triangular AL spot; lower margin of S4-S7 have obscure ML spot, very inconspicuous on S7. Ventrally, base of S4-S6 have a pair of sub-rectangular spots. Middorsal carina present on apical half of S3 to S7. Auricle broader and more well developed than in *O. lieni*. Shape of male cerci is unique among the known *pryeri*-group *Oligoaeschna* species, very long and about as long as S9 + S10, in oblique view, like a razor knife with basal 1/4 stalked and apical 3/4 abruptly expanded (Figs 7-9). Apical expansion of male cerci equal in width and strongly ridged dorsally; inner margin with round apex slightly protruding inward, convex dorsally and concave ventrally; apex of cerci pointed and directed postero-ventrally. Epiproct elongate, about half as long as cerci; apical emargination of epiproct shallow, with notched depth 1/7 as long as epiproct (Fig. 10).

FEMALE unknown.

VARIATION IN PARATYPES. – Paired spots of vertex smaller, about half size of median ocellus. Dorsal stripes connected, or somewhat connected, with spots above it in two specimens. Lateral yellow patches of S1 clearly defined in one specimen. Ventral sub-rectangular spots of S4-S6 vestigial in one specimen and almost invisible in another one (both collected in 18-VI-1996). Nodal index 7-8: 16-17: 15-17: 6-9 in forewings, 8-10: 11-12: 11-12: 9-10 in hindwings. Triangles two- or three-celled (2: 10, N = 12); anal loops three or five-celled (5: 1, N = 6); anal triangles three--celled in one specimen and four-celled in the other two.

Measurements (mm). – Holotype ♂: abd. + cerci 48, hindwing 37, pterostigma of forewing 3.0 and hindwing 3.1; paratypes 3♂: abd. + cerci 49-52, hindwing 37-39, pterostigma of forewing 3.0-3.1 and hindwing 2.9-3.3.

REMARKS. – All specimens of *O. tsaopiensis* were collected from its type locality only, but whether or not the population of this species is breeding at the bog is still doubtful, since neither larvae nor reproductive activity of female were observed. Further investigations are needed to confirm its syntopic existence with *O. lieni*, and also to unravel the ecological and biogeographical interaction between them.

NOTES ON *O. PYANAN* ASAHINA BASED ON THE SPECIMENS IN THE INSECT COLLECTION OF TARI

For comparison with the two new *Oligoaeschna*, some unstudied specimens of *O. pyanan* preserved in the Insect Collection of Taiwan Agricultural Research Institute (TARI) were located and checked.

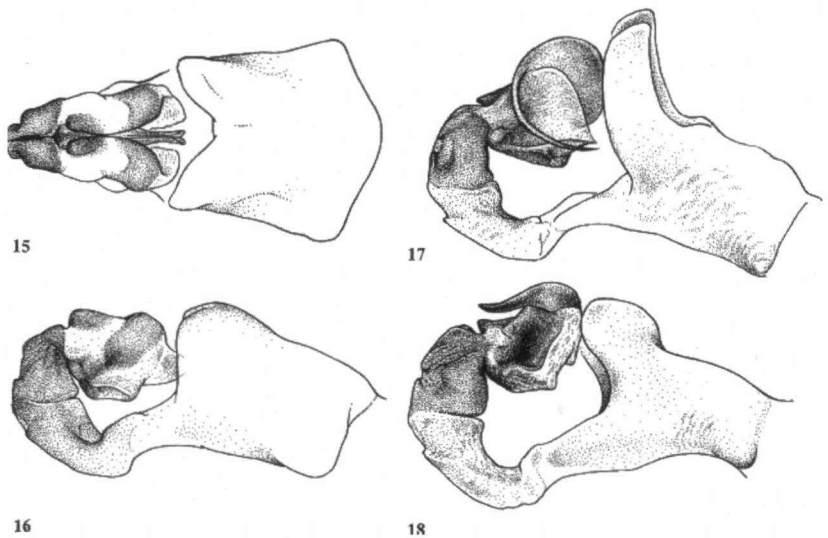
2♂: Miharasi (original collector?) on Mt Taiheizan [presently Mt. Taipingshan, 1950 m, Ilan county], N. Formosa, 19-VII-1940, coll. M. Chûjô; 1♂(checked but not studied): Sozan [presently Yangmingshan, Taipei city, northern Taiwan], Formosa, 16/18-VII-1938, collector unknown; 1♀: Taihoku [presently Taipei, exact locality uncertain], Formosa, 14-V-1926, collector unknown.

The general characters of these specimens coincide well with those given by ASAHINA (1951 & 1962) and LIEFTINCK (1968), but some variations are noted as follows: paired spots of vertex present in all three specimens, remarkable and broadly merged medially in the female. PD spots of abdomens present on S2-S6 or S7 in male and S2-S7 in female; MD spots present on S2-S3 in male and S2-S4 in female; ML spots present on S3-S7. Triangles three to five celled; anal loops five or six celled; anal triangles two or three celled in male. Measurements (in mm) of these specimens read as follows: Abdominal length (abd. + cerci) 45-50 in males and 48 in female; hindwing length 40-42 in males and 41 in female; length of pterostigma 2.7 in males and 2.9 in female.

It is worth mentioning here that, although *O. pyanan* has been generally considered to be a highland species (LIEFTINCK et al., 1984) with 1400 m the lowest known altitudinal record (KISHI, 1996), its present altitudinal range can be extended downward to at least below 1000 m by the records of the male and female collected from the Taipei area.

NOTES ON THE STATUS OF *PRYERI*- GROUP *OLIGOAESCHNA* FROM THE VIEW POINT OF MALE PENILE GLANS STRUCTURES

The penile glans of eastern Asian *pryeri*-group *Oligoaeschna* share several homologous structural similarities with those in the genus *Gomphaeschna*, which is from the fossil record considered to be the most primitive genus of extant aeshnids (WIGHTON & WILSON, 1986). The synapomorphies of penile glans structure uniting *Gomphaeschna* and eastern Asian *pryeri*-group *Oligoaeschna* (Figs 17--19) are: glans is complicated in shape and notched at lateral sides; medially embedded flagella strongly developed and ramhorn or sickle-shaped; anterior side of flagella covered with spine-like microstructures (Fig. 20), which are probably



Figs 15-18. Penis and sperm vesicle of *Gomphaeschna* and *Oligoaeschna*; 15 ventral view; 16-18 right lateral and ventral views: (15 & 16) *O. foliacea*; – (17) *G. furcillata*; – (18) *O. tsaopiensis* sp. n.

involved in inter-male sperm competition; base of glans ventrally with a pair of protruding and heavily sclerotized "bony plates". On the other hand, the penile glans of *poeciloptera*-group *Oligoaeschna*, as seen in *O. foliacea* (Figs 15, 16), is simple in shape, being hollow medially and not notched laterally; the ventrobasal bony plates are suppressed into a pair of deeply coloured patches and the apical flagella are vestigial and filament-like. The shape of the sperm vesicle (basal or first segment of "vesicula spermalis") in the *pryeri*- and *poeciloptera*-group *Oligoaeschna* is also different. In the former, the sperm vesicle is broadly hollow on ventral side, with flat bottom and markedly projecting ventral flange (cf. also KARUBE 1998a, 1998b); while in the latter, the hollow is narrower and the ventral flange more poorly developed. In *Gomphaeschna*, the sperm vesicle is narrowly notched ventrally, but the ventral flange is strongly protruding ventrad and developing into a pair of remarkable hooks. The different shapes of sperm vesicle amongst these genera are evidently co-evolved with the shapes of their flagella as a protected apparatus.

Although only a few species of *Oligoaeschna* were checked in the present study, the above results strongly suggest that the *pryeri*-group is in fact more closely related to the genus *Gomphaeschna* rather than to the *poeciloptera*-group, and its present taxonomic position within the genus needs further consideration. It may be worth of establishing a new separate genus for it.

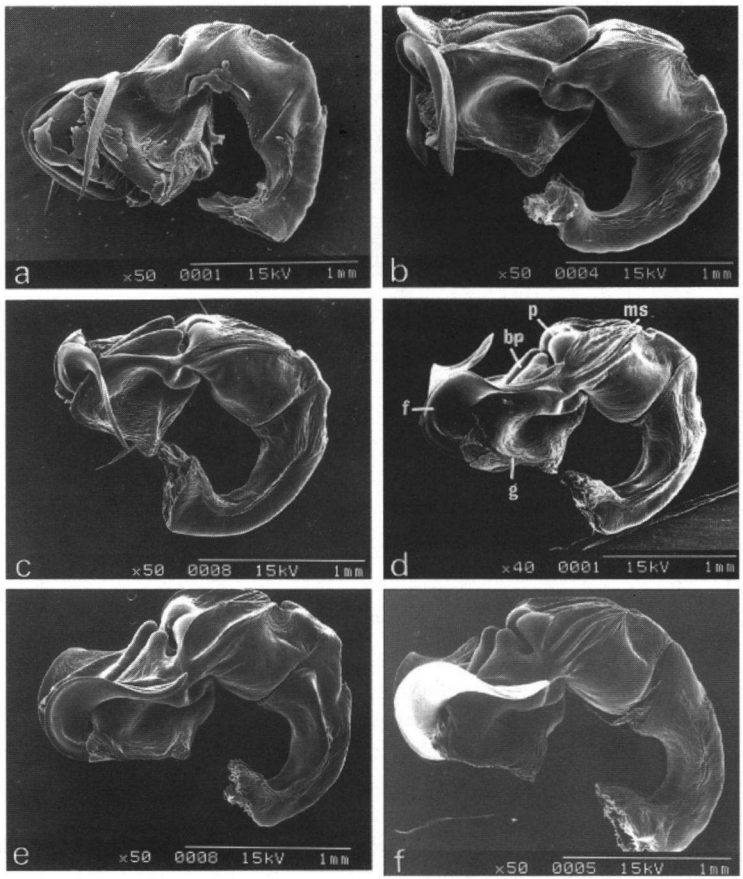


Fig 19. SEM pictures showing penile structure of *Gomphaeschna* and eastern Asian *pryeri*-group *Oligoaeschna*, left lateral and ventral views: (a) *G. furcillata*; – (b) *O. pyanan*; – (c) *O. lieni* sp. n.; – (d) *O. pryeri*; – (e) *O. kunigamiensis*; – (f) *O. tsaopiensis* sp. n. – [g – glans; f – flagella; ms – microsculptures of penile S3; p – ventroapical protuberance of penile S3; bp – ventrobasal bony plates of glans]

DISCUSSION

The highly different shapes of male cerci amongst the three species of Taiwanese *Oligoaeschna*, viz. *O. lieni*, *O. pyanan* and *O. tsaopiensis*, suggest that they do not form a closely related group, and this is also reflected by the differentiation of their penile structure (Fig. 19 & Tab. I). According to ASAHINA (1951, 1972), the diagnostic characters of *O. pyanan* include the peculiar shape of male cerci with pointed apex and marked ventral emargination, two rows of cells between MA & Mspl and the two-celled anal triangle. The second character shared by *O.*

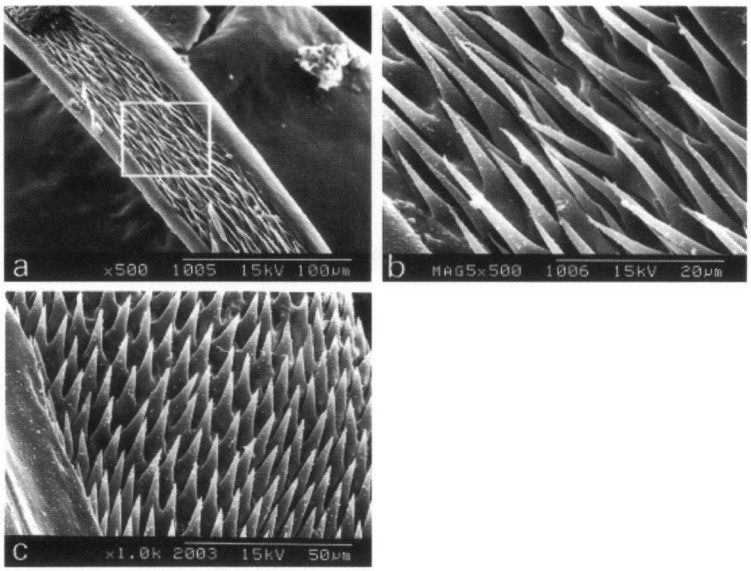


Fig 20. Spine-like microstructures on flagella of *Gomphaeschna* and eastern Asian *pryeri*-group *Oligoaeschna*: (a & b) *G. furcillata*; – (c) *O. pyanan.*

kunigamiensis (Ishida) has been pointed out by ASAHINA (1972), but his comment is not recognized by us in the specimens of the latter species examined. The third character is invalid, since it is variable individually, as demonstrated in the above noted variation. Close inspection of three specimens in TARI, however, reveals that *O. pyanan* is not closely related to the other eastern Asian species of the *pryeri*-group. Judging from its penile flagella, which in lateral view are perpendicular to glans (laterally crossing glans in *O. lieni*, and parallel to glans in *O. pryeri*, *O. kunigamiensis* and *O. tsaopiensis*), this species may correlate with *O. speciosa* (KARUBE, 1998a), a Himalayan ally. Two additional distinct characters of *O. pyanan*, not shared by other eastern Asian *pryeri*-group *Oligoaeshna*, are the obsolete middorsal carina of abdomen and the poorly developed auricles being about 1/2-2/3 in size of those of its eastern Asian allies.

Close relationship of *O. tsaopiensis* with its two Japanese allies, viz. *O.pryeri* and *O. knuigamiensis* (hereafter acronymized as KPT group) is supported by the penile character states a- MT, c- P, d- S, e- G, and f- TC, as shown in Figure 19 and tabulated in Table I.Within this group, *O. tsaopiensis* shares several characters in colour patterns with *O. kunigamiensis*, including dark labrum without paired yellow spots, dark brown pterogstigma and dark area of anteclypeus being more extensive (covering upper 5/6 of anteclypeus in *O. tsaopiensis* and *O. kunigamiensis* and 4/6 in *O. pryeri*), but only the first characters are possibly synapomorphic. There is also a linear transformation in the shape of male epiproct in this group from the

Table I
Penile character states of eastern Asian *pryeri*-group *Oligoaeschna*

Characters/species	*pyanan*	*lieni*	*pryeri*	*kuniga-miensis*	*tsaopi-ensis*
(a) twist of flagella; (F) flat, (ST) slightly twisted, (MT) markedly twisted	F	ST	MT	MT	MT
(b) curvature of flagella; (S) strong, (M) moderate	S	M	M	M	M
(c) relative position of flagella to glans; (P) perpendicular, (C) crossing, (L) parallel	PE	C	P	P	P
(d) ventroapical protuberance of penile S3; (O) obsolete, (M) moderate, (S) strong	O	M	S	S	S
(e) micro- sculptures of penile S3; (V) vestigial, (S) striate, (G) grooved and present at lateral sides	V	S	G	G	G
(f) ventrobasal bony plates of glans; (CC) compressed and crest-shaped, (CF) compressed and fin-shaped, (TC) tumid and cone-shaped	CC	CF	TC	TC	TC

longer and apically shallowly emarginate type of *O. tsaopiensis* to the shorter and apically strongly divaricate type of *O. pryeri*. The shape of male epiproct of *O. kunigamiensis* is more or less intermediate between the above two types. However, *O. pryeri* and O. *kunigamiensis* are undoubtedly more closely related to each other than each is to *O. tsaopiensis* in sharing the short and spatulate male cerci, which is given more weight than the shared dark labrum of the latter with *O. tsaopiensis* in the present analysis.

The affinity of *O. lieni* within eastern Asian *pryeri*-group *Oligoaeschna* is somewhat unclear, since it has the intermediate type of penile structure between the species of KPT group and *O. pyanan*. It may be an annectant species, or a member of still unrecognized group that connect the KPT group to *O. pyanan* and its allies.

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