An unusual species of spoon-wing lacewing (Neuroptera: Nemopteridae) from South Africa, with notes on its biology

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ABSTRACT. An unusual species of spoon-wing lacewing, Palmipenna aeleoptera sp.n., is described from Namaqualand, South Africa. This small species is similar to its three congeners in general body morphology and genitalic features. Its hindwings, however, differ dramatically from known insect hindwing form. These conspicuously pigmented wings with their relatively huge surface area are hypothesized to have dual aerodynamic and semaphore functions when used by males in gliding flight during mate attraction.

Introduction

The Nemopteridae are lacewings (Neuroptera) characterized by extraordinary modifications to the hindwings. Of the two subfamilies, the Crocinae comprises small insects with pale, much attenuated hindwings, while the Nemopteridae also possess elongate hindwings but these are broader than those of the Crocinae, and usually bear some form of apical modification. This can take the form of a spiral twist, or more frequently a combination of a laterally expanded region associated with a spiral twist.

The South African Nemopterinae comprises eleven genera, containing about 45% of the world's fauna (Tjeder, 1967). The winter-rainfall region of the south-western Cape supports a particularly rich nemopterid fauna characterized by a high degree of endemism (Picker, 1984). The genus Palmipenna Tjeder was erected for three species of small aberrant nemopterines restricted to Namaqualand (Tjeder, 1967). They form a natural group characterized by the presence of small eyes, and stout antennae divided into a proximal, bristle-bearing region, and a setiferous flagellum. The forewing venation is rather open, and the pterostigma small. In the females the costal cross veins are covered by oval pigment blotches. The form of the hindwings represents an unusual departure from the conventional nemopterine pattern. In Palmipenna they are short and terminate in a richly pigmented twisted paddle, which contrasts with the pale apical tip and proximal stalk of the hindwing. The fore tibiae lack a feature present in all other South African genera – a patch of pale setae covering the apical ventral surface. P.palmula and P.dilatans are known only from single collections, while P.pilicornis has been collected from a few localities (Tjeder, 1967). Most of the Palmipenna habitats are situated at high altitudes, and some may even receive snow cover in winter, e.g. the Matroosberg at 1070 m (Tjeder, 1967).

This paper describes a new unusual species of Palmipenna from the Biedouw Valley, Namaqualand. Information on the biology and flight behaviour is given. A suggested function for the hypertrophied hindwings is provided.

Palmipenna aeleoptera sp.n. (Figs. 1–17)

Measurements from type specimens are given in mm and were taken from alcohol-preserved specimens except for some wing measurements which were taken from dried specimens.
Head (Figs. 1–6). Frons and rostrum dark yellow, tip of labrum tan. Clypeus with transverse folds. Genae darker yellow. Rostrum long, 3.5×eye diameter. Mouthparts (Figs. 3–5) tan, excepting labial and maxillary palps which are dark tan proximally and shade to black distally. Intersegmental junctions unpigmented, resulting in a banded pattern. Head virtually free of hairs save for a patch on the dorsal ridge of the ocular diaphragm and scattered hairs on each side of the vertex. Vertex, dorsal and posterior aspects of head bright ochre, this coloration extending down to antennal scape. Antennae short and stout (0.36×forewing length in females; 0.42×forewing length in males). Proximal region ochre, and bearing long bristles; distal region olive-grey and covered in fine setae (Fig. 6). Sexual dimorphism evident in various antennal characters. Males have longer antennae, bearing a greater number of antennal segments than females (Table 1). In males a far greater proportion of the antenna comprises setaceous segments, with relatively few bristle-bearing segments. Females have a similar number of bristle and setae-bearing segments (Table 1). Terminal antennal segment pointed in both sexes, but more acute in the male.

Prothorax in male short, collar-like, and coloured tan: divided by a thin medial brown line surrounded laterally by light tan areas and then

FIGS. 1–5. Palmipenna aeoleoptera sp.n. Head and mouthparts of ♂. 1. Head (frontal view). 2. Head (lateral view). 3. Right mandible (dorsal view). 4. Left maxilla (ventral view). 5. Labium (ventral view). fr, frons; fs, frontal suture; atp, anterior tentorial pit; g, gena; cl, clypeus; fgs, fronto-genal suture; lbr, labrum; md, mandible; co, cardo; stp, stipes; mp, maxillary palp; lp, labial palp; pf, palpifer; bga, basigalea; dga, distigalea; pg, palpiger; lg, ligula; lc, lacinia.
by longitudinal dark brown bands. Lateral regions sulphur yellow. A row of long black setae runs along the anterior and posterior edge of the pronotum, and extends into the yellow regions of the prothorax. Prothorax of female very similar to that of the male, but dark brown stripes of lighter intensity.

Mesothorax coloured deep ochre in the male, with thin median brown stripe most vivid over the prescutum. Antero-lateral regions of prescutum deep brown, and continuous with similarly-pigmented areas of the prothorax and mesoscutum, forming a pair of lateral stripes along the thorax. Long black hairs present laterally, and centrally in the more posterior region. Mesoscutum ochre, with a pair of brown lateral stripes which bear long dark hairs mediolaterally in some males. Postnotum sulphur yellow with median longitudinal brown markings devoid of bristles. Metathorax of female very similar to that of the male, but having fainter longitudinal brown stripes, and a greater number of bristles, which are only half the length of those found in males. Entire lateral region of thorax sulphur yellow.

Metathorax very short and collar-like. Metascutellum large and lobe-like, ochreous, with central brown stripe continuous with that of the prothorax and mesothorax. Black bristles often present antero-laterally; longer in male.

TABLE 1. Means and ranges of selected characters of type specimens of *P.aeoleoptera*. All measurements in mm (ranges in parentheses).

<table>
<thead>
<tr>
<th></th>
<th>Male</th>
<th>n</th>
<th>Female</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body length</td>
<td>8.06 (7.4–8.4)</td>
<td>5</td>
<td>9.57 (7.7–11.1)</td>
<td>18</td>
</tr>
<tr>
<td>Antennal flagellum length</td>
<td>5.93 (4.9–7.3)</td>
<td>14</td>
<td>4.94 (4.2–5.7)</td>
<td>20</td>
</tr>
<tr>
<td>Total no. of antennal segments</td>
<td>32 (30–34)</td>
<td>15</td>
<td>27.8 (25–32)</td>
<td>17</td>
</tr>
<tr>
<td>No. of bristle-bearing antennal segments</td>
<td>9.9 (8–11)</td>
<td>15</td>
<td>14.2 (12–17)</td>
<td>17</td>
</tr>
<tr>
<td>No. of setae-bearing antennal segments</td>
<td>22 (20–25)</td>
<td>15</td>
<td>13.5 (11–16)</td>
<td>17</td>
</tr>
<tr>
<td>Eye diameter</td>
<td>0.24 (0.2–0.27)</td>
<td>19</td>
<td>0.24 (0.2–0.27)</td>
<td>20</td>
</tr>
<tr>
<td>Rostrum length</td>
<td>0.79 (0.68–0.9)</td>
<td>18</td>
<td>0.87 (0.7–0.95)</td>
<td>20</td>
</tr>
<tr>
<td>Forewing length</td>
<td>13.96 (12.5–15.4)</td>
<td>20</td>
<td>13.82 (11.4–15.7)</td>
<td>20</td>
</tr>
<tr>
<td>Forewing breadth</td>
<td>5.12 (4–6.6)</td>
<td>20</td>
<td>5.63 (4.7–6.8)</td>
<td>20</td>
</tr>
<tr>
<td>Hindwing length</td>
<td>17.08 (12.1–20.5)</td>
<td>20</td>
<td>15.62 (13.4–19.7)</td>
<td>20</td>
</tr>
<tr>
<td>Hindwing stalk length</td>
<td>4.54 (3.4–5.19)</td>
<td>20</td>
<td>5.57 (4.5–6.6)</td>
<td>20</td>
</tr>
<tr>
<td>Hindwing dilation length</td>
<td>12.55 (8.7–15.8)</td>
<td>20</td>
<td>10.45 (8.4–13.4)</td>
<td>20</td>
</tr>
<tr>
<td>Maximum diameter of hindwing</td>
<td>8.55 (6.5–13.3)</td>
<td>19</td>
<td>7.7 (5.9–13.2)</td>
<td>20</td>
</tr>
</tbody>
</table>
FIG. 7. Paratype ♂ and ♀ Palmipenna aeoleoptera. ♂♂ on left hand side. Note sexual dimorphism in hindwing (dilations flattened to show shape and venation).

Legs relatively long, pale citrine, and evenly covered in short black setae. Tarsi long; proximal tarsomere longer than combined length of other tarsal segments. Paired tarsal claws black, but pale at point of attachment to tarsomere. Sexual dimorphism absent.

Forewing venation and shape as in other Palmipenna species (Fig. 7). 14–18 costal cross veins before pterostigma (x = 15.85, n = 20). Membrane hyaline; pterostigma small, pale yellow. Conspicuous oval pigment deposits situated over proximal costal cross veins in female. Venation dark brown, save for subcosta and radius which are light brown. Although the forewing length of the male is not significantly different from that of the female (P > 0.2, paired t-test, Table 1), females have significantly broader forewings (P < 0.01, paired t-test, Table 1).

Hindwing facies unique amongst the Nemopteridae (Fig. 7). Slightly longer than forewing, and shaped like an asymmetrical leaf, with a short stalk before the dilation (pronounced in males), dilation with a broad horizontal surface and a medial vertical flange representing the atrophied helical twist found in other nemopterine genera. Venation dense, with numerous cross veins and marginal forking. Females having much smaller dilations that the male (Table 1). Hindwing stalk significantly shorter in males than females (P < 0.0005, paired t-test, Table 1), even though the total hindwing length does not differ significantly between the sexes (P > 0.05, paired t-test, Table 1). However, in the male the dilation occupies a significantly greater proportion of the total hindwing length (P < 0.0005, paired t-test, Table 1). Both sexes have similar largest diameters of the dilation. Venation pale brown. Stalk ochre; dilation patterned in light and dark brown, relieved by cream-white patches. In some males hindwings very dark brown – this effect produced by deep pigmentation of areas adjacent to veins. Some polymorphism exists with regard to the lighter regions; in their full expression they comprise a postero-medial crescent in the anal region, and another patch opposite this in the costal region very close to the pterostigma. A characteristic cream oval is always found in a cell formed by the terminal bifurcation of the subcosta. In general females have paler hindwings than males, especially at the proximal end of the dilation and area between radius and media.

Abdomen (Figs. 8–12) relatively short and stout (longer in female), appearing bicoloured, with ochre tergites contrasting with the citrine sternites. Pleurites divided longitudinally into a dorsal brown and ventral pink region. Abdomen
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FIG. 12. *Palmipenna aeoleoptera* sp.n. Abdomen of ♀ (lateral view). 5, 6, 7, 8 and 9, tergites; epr, ectoprocts; cc, callus cerci; go la, gonapophyses lateralis; S7, S8, sternites.

covered in many short black hairs (which are similarly distributed in both sexes). In the male (Figs. 8–11) posterior margin of tergite 5 pleated, forming opening for a pair of conspicuous pleuritocavae which when inverted project anteriorly. Tergite 9 divided into two narrow halves each having a marginal row of short black bristles. Ectoprocts bulbous, bearing a dorso-medial and ventral row of bristles. Callus cerc inconspicuous and devoid of hairs. Sternite large, projecting beyond origin of tergite 9, at bearing a row of long, stout bristles on posterior margin. Gonarcus similarly shaped to that other *Palmipenna* species. Gonarcus ar
FIG. 13. Egg of *Palmipenna aeleoptera*. Entire egg showing cap covering micropylar region. Note smooth egg chorion.

relatively narrow, bearing two conspicuous patches of gonosetae. Parameres in lateral view having near right angle bend; in posterior view of arrowhead shape. Female (Fig. 12) having ectoprocts with indistinct callus cerci and relatively dense long hairs laterally. Gonolatus lateral is shaped as in other *Palmipenna* species, and covered in very dense long black hairs on lateral margins. Tergite 9 widest ventrally.

Egg (Fig. 13). Most of the captured females were gravid, and oviposited after a week in captivity, glueing eggs to vertical surfaces. Eggs oval, somewhat elongate, with no obvious surface sculpturing, 1.04 mm long ($n=6$). The terminal micropyle is covered by a small cap pierced by numerous holes.

Type material. *Holotype* ♂, SOUTH AFRICA: Cape Province, Biedouw Valley, 70 km east of Clanwilliam, Namaqualand (32°05'S, 19°15'E), 7.ix.1985 (Picker) (NCI). *Paratypes*. 2♂ ♂, 3♀ ♀ (NCI), 2♂ ♂, 2♀ ♀ (SAM), 2♂ ♂, 2♀ ♀ (BMNH), 2♂ ♂, 2♀ ♀ (ZML), 1♂, 1♀ (AMNH), data as for holotype.


*Habitat.* *P. aeleoptera* was locally common on certain north-facing broken slopes in the wind sheltered Biedouw Valley (Fig. 14). The locality is in southern Namaqualand, an area renowned for its vernal flush of flowering annuals and *Mesembryanthemaceae*. The dominant plant species in flower at the time of capture of

FIG. 14. Habitat of *Palmipenna aeleoptera*, Biedouw Valley, Namaqualand. The habitat comprises broken rock interspersed with open sandy patches. A succulent community dominates the flora.
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FIG. 15. ♀ Palmipenna aeoleoptera resting on the mesembryanthemum Ruschia geminiflora. This was the major pollen source for P.aeoleoptera.

P.aeoleoptera was the mesembryanthemum Ruschia geminiflora (although it was not present in all areas where the insects were caught). The insects became active at about 10.30 hours, when ambient temperatures reached 33°C. They were nearly always found resting on the ground or rocks.

Biology and behaviour. Field observations

FIG. 16. Antennal base of ♀ Palmipenna aeoleoptera. Two types of pollen grain were found adhering to the head.
FIG. 17. ♂ *Palmipenna aeoeloptera* hindwings showing the formation of a horizontal gliding surface and vertical vane by apposition of the wings. (a). Normal resting and flight position of hindwings. (b). Apposed hindwings (dorsal view). (c). Apposed hindwings (posterior view).

(6–7.ix.85) showed that the insects spent most of their time resting on the substrate, frequently twitching the hindwings and raising them vertically. The flight duration of females was very brief (\( \bar{x} = 0.7 \) s (0.25–1.5 s), \( n = 77 \); B. Leon, pers. comm.), while the flight duration and distance covered in single flights by males was far longer (lasting many seconds), and for this reason was difficult to quantify. The skewed sex ratio of captured insects (23 males; 40 females) probably reflects this difference in flight ability between the sexes. At approximately 16.30 hours many individuals (mostly females) moved onto the flowering mesembryanthemum *R. geminiflora* and began feeding on the pollen (Fig. 15). The flowers of this shrub had been open all day. Scanning electron micrographs of the head reveal the presence of two kinds of pollen grain (Fig. 16). Males patrolled the periphery of bushes, but no mating behaviour was
observed. Both males and females twitched and 'batted' their hindwings while resting, but no interactions were noted between individuals. Males were capable of rapid, sustained flight, and were noted on a few occasions to slow down and indulge in gliding flight. A single, clear field observation (at 12.00 hours), and several laboratory observations revealed that in gliding the hindwing stalks are held parallel to one another. This results in the juxtaposition of the hindwings such that the two median portions appose to form a single vertical vane. In this position the rest of the hindwings form a horizontal aerofoil, the resultant combination resembling the tailfin of an aeroplane (Fig. 17). A male was observed in the field at very close range aligning the hindwings as described above. Every few seconds the horizontally-disposed forewings would vibrate with small amplitude, resulting in effective gliding with little loss in altitude.

Discussion

_P.aeoleoptera_ closely resembles its three congeners in general body morphology, including genitalic features. It has in common with other _Palmipenna_ species well-developed eversible vesicles, which are presumed to be pheromone-producing organs (Tjeder, 1967). However, no male _P.aeoleoptera_ were captured with everted vesicles and the only observation by the author of the eversion of these saclike structures was in a male of a related genus, _Nemopterella_. _P.aeoleoptera_ is the smallest _Palmipenna_ species, and has fewer antennal segments in the male than other congeners. Its hindwings, however, differ dramatically from other _Palmipenna_ species, and represent an unusual departure from known insect hindwing morphology. The nearest parallels (besides the three congeners) are found in certain Lepidoptera. Occasional papilionids and hesperids have attenuated hindwings (Lewis, 1973), while among the moths _Eustera_ species (Saturniidae) have very elongate hindwings and _Semioptila_ species (Zygaenidae-Himanopterinae) have elongated hindwings incorporating a terminal dilation (Pinhey, 1975). It is among the Nemopteridae, however, that this unusual hindwing modification reaches its acme, and presents a synapomorphy for the entire family. Among the Nemopterinae, _Palmipenna_ species have the greatest hindwing surface area. Of the three previously described species, _P.palmulata_ has the largest dilation, but this is only about one third that of _P.aeoleoptera_. Not only are the hindwing dilations of _P.aeoleoptera_ considerably larger in the male than in the female, but they also have far darker pigmentation. This trend is also evident in _P.palmulata_. The function of such conspicuously developed structures is not, however, immediately evident, and various roles have been attributed to them (Tjeder, 1967; Picker, 1984). A cryptic role seems unlikely in view of the conspicuous nature of the hindwings when viewed in nature (albeit by human observers). Moreover, large surface area dried leaves which might match the appearance of the hindwings are virtually absent in the succulent-dominated habitat of _P.aeoleoptera_. An alternative function for these pigmented wings endowed with a haemolymph supply – that of solar absorbers – has been tested under laboratory conditions, and the results show little support for a thermo-regulatory role (B. Leon and M. D. Picker, in preparation).

A far more likely function for the hindwings, gaining support from both field and laboratory observations, is that of semaphores which, at least in the males, may have a significant aerodynamic role in gliding flight. Limited field observations, coupled with obvious sexual dimorphism in these structures, tends to support this hypothesis (sexual dimorphism of this kind is marked in many other nemopterids; Tjeder, 1967). Such gliding flights by males may be associated with courtship swarms, or a form of patrolling flight used in territorial behaviour. Such an adaptation would enable males to save energy while advertising their presence and readiness for mating to receptive females. Although very little is known about nemopterid mating behaviour, mating swarms have been reported in the Crocinae (Imms, 1911; Hafez & El-Moursy, 1965; Sullivan, 1981). It is thus suggested here that the use of the hindwings in _P.aeoleoptera_ represents an hypertrophication of a pattern present in all nemopterids, where the hindwings have some aerodynamic role. The only information available to the author on the use of elongated hindwings in insects derives from observations of Nachtigall (1974) on the 'sail' butterfly, _Iphiclides podalirius_, which is capable of sus-
tained gliding flights of up to 10 m. He suggests that extensions of lepidopteran hindwings facilitate limited gliding flight. Although small gliders with rounded wings are theoretically unable to develop significant gliding powers as a result of the unfavourable aspect ratio (Nachtigall, 1974), P.aeoleoptera may well overcome this limitation by using the very large hindwing surface area in combination with thermals generated from heated ground and rocks.

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References


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