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Srivari Illam, No. 61, Karthik Nagar, 10th Street, Saravanampatti, Coimbatore, Tamil Nadu 641035, India  
Registered Office: 3A2 Varadarajulu Nagar, FCI Road, Ganapathy, Coimbatore, Tamil Nadu 641006, India  
Ph: +91 9385339863 | [www.threatenedtaxa.org](http://www.threatenedtaxa.org)  
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Cover: A male Scarlet Skimmer perching on vegetation by the banks of a waterbody. Ink and watercolour illustration by Ananditha Pascal.



## A preliminary investigation on wing morphology, flight patterns, and flight heights of selected odonates

Ananditha Pascal<sup>1</sup>  & Chelmala Srinivasulu<sup>2</sup> 

<sup>1,2</sup> Wildlife Biology and Taxonomy Lab, Department of Zoology, University College of Science, Osmania University, Telangana 500007, India.

<sup>1,2</sup> Centre for Biodiversity and Conservation Studies, Osmania University, Telangana 500007, India.

<sup>1</sup> anandithaa2001@gmail.com, <sup>2</sup> chelmala.srinivasulu@osmania.ac.in (corresponding author)

**Abstract:** Wing shape and its individual structural components are a major contributor to the flight performance of odonates. Two essential components of wing structure are the nodus and the pterostigma. Our study showed that the position of the nodus (expressed as the nodal index) in the forewings and hindwings of dragonflies show subtle, but functionally important differences, whereas on a broader scale, dragonflies and damselflies show characteristic differences in accordance with their specific flight requirements. The position of the pterostigma expressed as the pterostigmatal index was observed to be optimized close to the wing tip across all odonates and unlike the nodus, there were no characteristic differences between dragonflies and damselflies in this regard. In addition to describing wing shape using aspect ratio, our study presents a geometric morphometric analysis of wing shape across flying and perching behaviour and across flight heights of odonates. It was found that wing shape does not significantly differ between fliers and perchers. However, certain species namely *Crocothemis servilia*, *Tholymis tillarga*, and *Gynacantha bayadera* showed notable deviations in wing shape. These deviations indicate that the dichotomous classification of odonates into perchers and fliers is too broad, possibly overlooking the nuanced flight patterns adopted by these insects. On the other hand, a significant association was found between wing shape and flight heights of odonates. These results suggest that behavioural factors may influence odonate wing shape, while also highlighting the importance of wing shape in flight efficiency. Consequently, the flight performance of biomimetic devices modelled after odonate flight, may be enhanced by optimizing wing shape in accordance with the heights above ground at which these devices are intended to operate.

**Keywords:** Aspect ratio, damselflies, dragonflies, Epiprocta, flight behaviour, geometric morphometrics, Nodal Index, Pterostigmatal Index, wing shape, wing venation, Zygoptera.

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**Author details:** Ananditha Pascal is an intern at the Centre for Biodiversity and Conservation Studies, Osmania University (OU), Hyderabad, India. Following the completion of her MSc in Zoology from the Department of Zoology, OU, she completed the Ram Hattikur Advanced Training in Conservation at Zoo Outreach Organisation (Coimbatore, India) as a 2024 fellow. Chelmala Srinivasulu is a professor of Zoology at Osmania University, Hyderabad, where he heads the Wildlife Biology and Taxonomy Lab and directs the Centre for Biodiversity and Conservation Studies. He researches biodiversity conservation, systematics, and taxonomy of mammals, reptiles, and birds, as well as climate-change modelling.

**Author contributions:** AP—methodology, formal analysis, investigation, writing original draft, visualization. CS—conceptualization, validation, resources, writing, review and editing, supervision, funding acquisition.

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## INTRODUCTION

The order Odonata, consisting of dragonflies (Suborder Epiprocta) and damselflies (Suborder Zygoptera), is comprised of 6,442 described species worldwide, with a near cosmopolitan distribution (Paulson et al. 2024). Odonates are characterized by their distinctive morphology, with adults exhibiting elongated bodies and complex veined membranous wings, which support their exceptional flight capabilities. These insects inhabit a wide range of habitats. India, in particular, hosts a high odonate diversity, with a total record of 504 species belonging to 17 families (Subramaniam & Babu 2024). Odonates are important contributors to ecosystem functioning and occupy an important position in the food web, both as predator and prey (May 2019). Adult odonates are voracious opportunistic predators, feeding on a wide variety of prey organisms, particularly small dipterans belonging to Chironomidae, Sciaridae, and Cecidomyiidae (Arnaud et al. 2022) and are hence, believed to contribute to natural pest control (May 2019), especially in riparian habitats. Their hemimetabolous life cycle, comprising of an aquatic larval stage and a terrestrial adult stage depends on the availability of good riparian microhabitats and hence, odonates have been studied as bioindicators for the monitoring of ecosystem health (Subramanian et al. 2008).

The aerodynamic performance of odonates, enabled by the distinctive morphology of their wings and powerful thoracic musculature, has been extensively studied (Wootton 2009; Fauziyah et al. 2014; Bomphrey et al. 2016; Rajabi et al. 2018; Wootton 2020), and widely explored as models for the development of biomimetic devices (Khaheshi et al. 2021a,b,c). A key factor contributing to their flight efficiency is the complex wing morphology (Wootton 1991). The nodus and the pterostigma are two key components of wing structure (Rajabi & Gorb 2020). Located between two leading-edge spars (the stiff antenodal spar and the flexible postnodal spar), the nodus serves as a one-way hinge that regulates wing deformations (Rajabi et al. 2017, 2018). The pterostigma serves as an inertial regulator of wing pitch, preventing structural damage from self-excited wing vibrations and raising the critical speeds of flight (Norberg 1972).

Wing shape plays a critical role in the aerodynamic performance of odonates, influencing flight mechanics, and energy efficiency. Understanding variation in wing shape is important, especially in the context of the various flight strategies that odonates adopt.

Odonates can be broadly classified into 'fliers' and 'perchers' based largely on distinct flight behaviours and thermoregulatory strategies used (Corbet 1980). Fliers are endothermic species that remain on the wing during active periods (patrolling, mating, and foraging), while perchers are ectotherms and spend most of their time on a perch, taking only short flights (Corbett & May 2008). These behavioural types also differ in their characteristic energy requirements, with fliers consuming more metabolic energy than perchers (Corbet & May 2008). Additionally, odonates have been observed to fly at various heights above the ground (Mitra et al. 1998; Miller 2007; Subramanian 2012), which may further influence energy consumption. Given that wing shape directly impacts aerodynamic performance and energy efficiency (Luo & Sun 2005; Shahzad et al. 2016; Fu et al. 2018), it can be hypothesized that wing shape will differ between flying and perching behaviours and across flight height preferences. Flight height in particular remains largely unexplored and not documented among odonates.

To better understand the variation in wing shape and to make a meaningful comparison across species, wing shape needs to be quantified. Aspect ratio (AR) is one of the most commonly used measures of wing shape in aerodynamics (Phillips et al. 2015) and a key morphological descriptor of a wing (Bhat et al. 2019). It is a critical factor influencing flight dynamics and hence, wing AR has been well studied to gain insights into the influence of wing shape on the flight performance of odonates and insects in general (May 1981; Wakeling 1997; Wakeling & Ellington 1997a,b,c; Johansson et al. 2009; Phillips et al. 2015; Li & Nabawy 2022). However, studies suggest that wing AR being a single numerical quantity is not a robust measure of wing shape (Wakeling 1997; Betts & Wootton 1998; Johansson et al. 2009). Addressing this limitation, geometric morphometrics (GM) has emerged as a robust tool, providing a multivariate description of wing shape (Johansson et al. 2009) as it is comprehensive enough to detect subtle, yet significant variations in wing shape (Hassall 2015; Tatsuta et al. 2018; MacLeod 2022; Tarrís-Samaniego et al. 2023; Xi et al. 2024).

## MATERIAL AND METHODS

The study sample consisted of 25 individual specimens belonging to 19 odonate species collected from Greater Hyderabad and deposited at the Natural

History Museum, Department of Zoology, Osmania University, Hyderabad, Telangana. Located on the Deccan Plateau, Greater Hyderabad covers an area of 650 km<sup>2</sup> and is one of the largest metropolitan areas in India. The city experiences a hot semi-arid climate, receiving most of its annual rainfall from June to October (Anon. 2024). Although being a landlocked region, Greater Hyderabad has a considerable number of lakes, both natural and man-made. Hyderabad's lakes along with its predominantly sloping terrain, supports a broad spectrum of biodiversity. However, due to a rapidly growing human population and subsequent urbanization, the city has lost about 61% of its lake area in last 44 years. Conservation initiatives and efforts continue to be made to preserve and restore the green cover and freshwater ecosystems.

Of the 19 species collected, 16 were dragonflies and three were damselflies (Table 1). The flight behaviour and the flight heights of the species were determined based on field guides, manuals, and research papers (Sakagami et al. 1974; Mitra 1994; Mitra et al. 1998; Mitra 2006; Miller 2007; Andrew et al. 2008; Corbet & May 2008; Subramanian 2012; Sharma & Oli 2022).

The wings of each individual specimen were photographed using a digital camera (Sony DSC-WX7). The wing length (WL), wing area (WA), distance of the nodus and distance of the pterostigma from the wing base of both the forewings and hindwings of each individual were measured using ImageJ ver. 1.54g (Schneider et al. 2012). Data obtained from the forewings and hindwings were analyzed separately throughout this study. For damselflies, only the forewings were considered for analyses.

The morphometric measurements obtained were then used to calculate the nodal index (NI), the pterostigmatal index (PI) and aspect ratio (AR). The NI was calculated as distance of the nodus from the wing base as a fraction of wing length (Wootton 2020), using the formula:

$$NI = \frac{\text{Distance of the nodus from the wing base (mm)}}{\text{Wing length (mm)}}$$

The PI was calculated as distance of the pterostigma from the wing base as a fraction of wing length, using the formula:

$$PI = \frac{\text{Distance of the pterostigma from the wing base (mm)}}{\text{Wing length (mm)}}$$

**Table 1.** List of species included in the study sample.

Family	Species	Flight behaviour	Flight height
Libellulidae	<i>Acisoma panorpoides</i>	Percher	Low
Aeshnidea	<i>Anax guttatus</i>	Flier	High
Libellulidae	<i>Crocothemis servilia</i>	Percher	Medium
Libellulidae	<i>Diplacodes trivialis</i>	Percher	Medium
Aeshnidea	<i>Gynacantha bayadera</i>	Flier	Medium
Gomphidae	<i>Ictinogomphus rapax</i>	Percher	Low
Libellulidae	<i>Orthetrum glaucum</i>	Flier	Medium
Libellulidae	<i>Orthetrum sabina</i>	Percher	Medium
Libellulidae	<i>Orthetrum taeniolatum</i>	Percher	Medium
Libellulidae	<i>Pantala flavescens</i>	Flier	High
Gomphidae	<i>Paragomphus lineatus</i>	Percher	Low
Libellulidae	<i>Tholymis tillarga</i>	Flier	Low
Libellulidae	<i>Tramea basilaris</i>	Flier	High
Libellulidae	<i>Tramea limbata</i>	Flier	Medium
Libellulidae	<i>Trithemis aurora</i>	Flier	Low
Libellulidae	<i>Trithemis pallidinervis</i>	Percher	Low
Coenagrionidae	<i>Ceriagrion coromandelianum</i>	Percher	Low
Coenagrionidae	<i>Ischnura senegalensis</i>	Percher	Low
Lestidae	<i>Lestes elatus</i>	Percher	Low

Wing AR was calculated as two times the square of wing length divided by wing area (Bhat et al. 2019), using the formula:

$$AR = 2 \left( \frac{\text{wing length}^2}{\text{wing area}} \right)$$

Regression tests were performed to determine the relationship between wing AR and flight behaviour, and wing AR and flight height.

A GM analysis of wing shape was performed to comprehensively analyse wing shape. A landmarks-based approach was adopted, wherein appropriate landmarks were placed on the digitized wing images (Figure 1) and the corresponding coordinates obtained using ImageJ software. The landmark-coordinates were standardized using generalized procrustes fitting. A procrustes ANOVA was then conducted to determine the statistical significance of wing shape differences among the groups being compared. Additionally, a principal component analysis (PCA) was performed to visualize patterns of variation and similarity in wing shape. All analyses were performed on MorphoJ ver. 1.08.02 (Klingenberg 2011).

## RESULTS

Obtained measurements of wing length and nodal distance from the wing base were used to calculate the NI. Dragonflies exhibit a NI range of 0.40–0.53 (Table 2) indicating a centred nodal position. Furthermore, the hindwing is consistently observed to have a lower NI compared to the forewing across all individual dragonflies. Damselflies on the other hand are observed to have a particularly low NI compared to dragonflies (Table 2). They exhibit a NI range of 0.32–0.37, indicating an extremely proximal nodal position.

Measurements of wing length and pterostigmatal distance from the wing base were used to calculate the PI. All odonates exhibit a PI range of 0.80–0.93, with no significant variation observed between dragonflies and damselflies (Table 2).

Wing AR was calculated from wing length and wing area. Among dragonflies, the forewings exhibit an AR range of 9.0–11.2, while the hindwings have an AR range of 7.2–8.5 (Table 2). The hindwings have a broad expanded anal lobe which lowers the AR compared to the narrower forewings. Damselflies on the other hand have particularly narrow wings and hence, exhibit

extremely high wing AR (Table 2).

Wing AR did not differ significantly between fliers and perchers (Regression test; non-significant; forewing AR:  $p = 0.293$ , hindwing AR:  $p = 0.592$ ) and across flight heights (Regression test; non-significant; forewing AR:  $p = 0.224$ , hindwing AR:  $p = 0.463$ ).

However, a GM analysis of wing shape provided notable results. While wing shape did not differ significantly between fliers and perchers (Procrustes ANOVA; non-significant;  $p = 0.141$ ), a significant association was observed between wing shape and the flight heights of odonates (Procrustes ANOVA; significant;  $p = 0.021$ ).

Additionally, the PCA plots for forewing and hindwing shape analysis of dragonflies (Figure 2b & c) revealed significant deviations in wing shape for certain species, namely *Crocothemis servilia*, *Tholymis tillarga*, and *Gynacantha bayadera*.

Although *Crocothemis servilia* is classified as a percher, its forewing shape appears to be closely similar to that of *Pantala flavescens*, a typical flier. On the other hand, its hindwing shape was found to significantly deviate from all related libellulids.

*Tholymis tillarga* and *Gynacantha bayadera* are

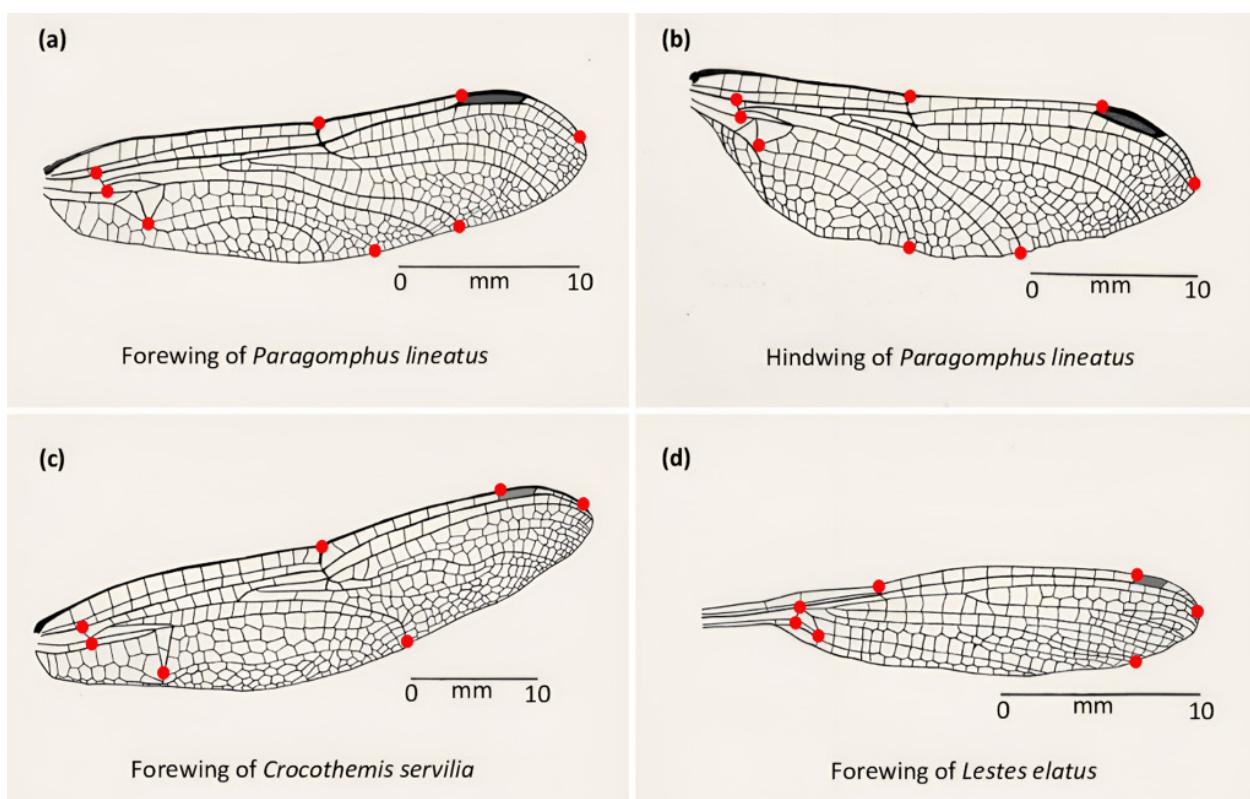
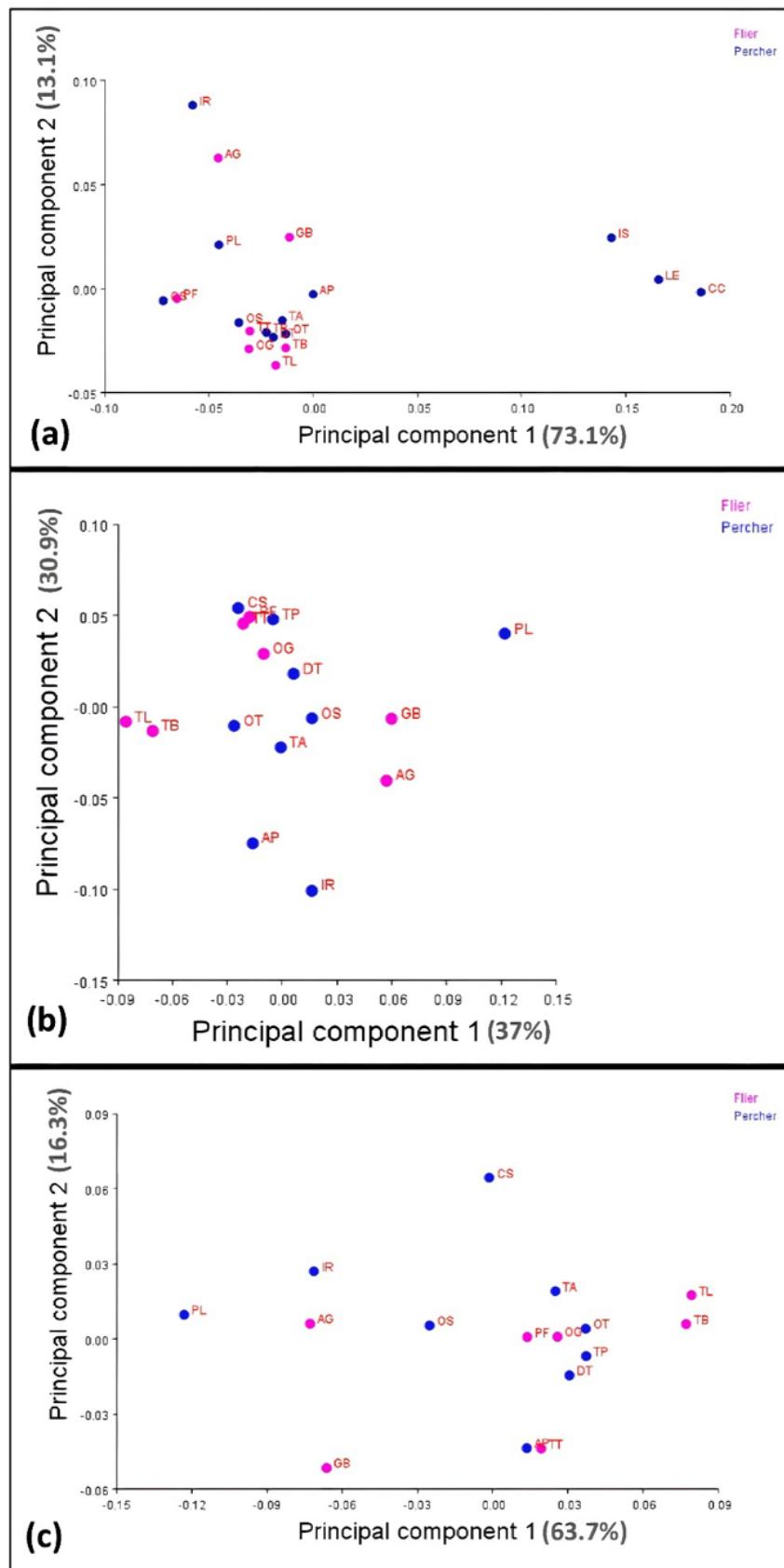


Figure 1. Landmark positions for: a—Forewing | b—Hindwing shape analysis of dragonflies | c&d—Forewing shape analysis of damselflies. Original drawings by Ananditha Pascal.



**Figure 2. Principal component analysis plots of: a—Forewing shapes of dragonflies and damselflies | b—Forewing shape of dragonflies | c—Hindwing shape of dragonflies**

**Table 2. Morphometric measurements of forewing and hindwing of Odonates.**

Species	Forewing					Hindwing				
	WL (mm)	WA (mm <sup>2</sup> )	AR	NI	PI	WL (mm)	WA (mm <sup>2</sup> )	AR	NI	PI
<i>Acisoma panorpoides</i>	19.725	85.648	9.086	0.469	0.878	19.626	104.937	7.347	0.417	0.857
<i>Anax guttatus</i>	53.837	554.288	10.458	0.496	0.805	51.691	659.963	8.097	0.418	0.791
<i>Crocothemis servilia</i>	45.953	375.438	11.249	0.533	0.879	41.652	412.128	8.419	0.403	0.877
<i>Diplacodes trivialis</i>	23.5455	119.052	9.381	0.478	0.891	23.192	149.171	7.254	0.445	0.893
<i>Gynacantha bayadera</i>	45.033	425.879	9.524	0.478	0.635	45.683	575.496	7.253	0.406	0.859
<i>Ictinogomphus rapax</i>	58.313	604.567	11.249	0.519	0.831	54.449	659.442	8.992	0.436	0.828
<i>Orthetrum glaucum</i>	31.758	202.603	9.956	0.508	0.908	31.813	256.175	7.901	0.486	0.912
<i>Orthetrum sabina</i>	36.15	250.017	10.481	0.489	0.878	34.580	292.737	8.239	0.452	0.883
<i>Orthetrum taeniolatum</i>	30.403	163.613	11.299	0.494	0.906	29.598	218.821	8.007	0.445	0.896
<i>Pantala flavescens</i>	40.187	308.330	10.476	0.530	0.878	40.184	420.816	7.674	0.434	0.873
<i>Paragomphus lineatus</i>	29.953	186.399	9.626	0.498	0.846	28.547	191.113	8.528	0.416	0.844
<i>Tholymis tillarga</i>	36.006	261.698	9.956	0.502	0.880	37.665	385.244	7.436	0.426	0.880
<i>Tramea basilaris</i>	43.941	381.812	10.114	0.503	0.932	44.689	498.008	8.020	0.438	0.909
<i>Tramea limbata</i>	41.699	330.970	10.507	0.494	0.922	43.596	460.122	8.261	0.441	0.924
<i>Trithemis aurora</i>	33.45	209.589	10.677	0.485	0.896	33.116	259.842	8.441	0.434	0.891
<i>Trithemis pallidinervis</i>	34.947	250.817	9.739	0.505	0.902	34.560	318.341	7.504	0.445	0.902
<i>Ceriagrion coromandelianum</i>	20.692	59.605	14.367	0.322	0.925	20.692	59.605	14.367	0.322	0.925
<i>Ischnura senegalensis</i>	14.517	32.504	12.967	0.370	0.891	14.994	34.840	12.906	0.364	0.936
<i>Lestes elatus</i>	24.405	84.647	14.073	0.357	0.912	24.405	84.647	14.073	0.357	0.912

WL—Wing length | WA—Wing area | AR—Aspect ratio | NI—Nodal index | PI—Pterostigmatal index.

crepuscular dragonflies. *Tholymis tillarga*, which belongs to the family Libellulidae and is classified as a flier, is observed to have a forewing shape similar to other libellulids such as *Pantala flavescens*, as expected. However, its hindwing shape appears to be closely similar to that of *Acisoma panorpoides*, which is a typical percher. *Gynacantha bayadera*, which is an aeshnid and is classified as a flier, significantly deviates in its hindwing shape from that of *Anax guttatus*, which is also an aeshnid and a flier.

## DISCUSSION

The objectives of our study were to record and compare the position of the nodus and the position of the pterostigma among members of different families of Odonata and to analyse wing shape in the context of flight patterns and flight heights.

The nodus is located between two leading-edge spars with distinct properties – the thick antenodal spar which provides stiffness and the flexible postnodal spar which is the principal area of wing torsion (Wootton

1991). Therefore, the position of the nodus determines the degree of wing torsion that can develop, thereby influencing the amount of lift generated during flight (Wootton & Newman 2008), and the NI which indicates the location of the nodus is useful to compare the species in this regard (Wootton 2020).

The results of the present study show that, in the case of dragonflies, the forewing nodus is positioned anywhere between 0.46 and 0.53 (approximately 50%) of the wing length from the base. On the other hand, it is observed that the hindwing nodus of dragonflies is positioned between 0.40 and 0.48 of the wing length from the base, i.e., less than 50% of the wing length. Additionally, when compared with the forewings, the hindwings have a low AR range, at which flight efficiency is low (Ennos 1988). However, it is likely that the hindwing's proximally positioned nodus, which allows for greater wing torsion and better aerodynamic lift (Ennos 1988; Wootton 2020), compensates for this reduced flight efficiency.

Unlike dragonflies, damselflies are found to have an extremely low NI of 0.3 on average. Such a proximally positioned nodus has been suggested to aid the

habitually slow flight characteristic of the families Coenagrionidae and Lestidae (Wootton 2020).

The PI(s) calculated in the present study indicate that the pterostigma is consistently positioned at around 0.80–0.93 of the wing length in both the forewings and hindwings, across all odonates. This supports the conclusion that for the pterostigma to contribute to efficient flight, it has to be positioned close to the wing tip (Norberg 1972). Unlike the position of the nodus, the position of the pterostigma did not show significant variation between dragonflies and damselflies.

The wing AR(s) calculated in the present study show that dragonfly forewings do not exceed an AR of around 10. This validates earlier studies which have suggested that aerodynamic efficiency is achieved at intermediate AR(s) of around 5 for a single wing (Ennos 1989; Phillips et al. 2015; Li & Nabawy 2022).

On the other hand, the damselflies have been observed to have high AR wings exceeding the AR of 5 for a single wing. At such high AR values, the amount of lift generated falls down significantly (Phillips et al. 2015; Li & Nabawy 2022). This is likely responsible for the lower flight heights of damselflies, compared to dragonflies.

Additionally, the present study found no significant relationship between wing AR and flying and perching behaviour, and wing AR and flight heights. This aligns with studies which found no significant association between wing AR and the flight patterns of odonates (Wakeling 1997; Johansson et al. 2009). This indicates that AR being a single numerical quantity may not be robust enough to quantify and detect subtle variations in wing shape (Betts & Wootton 1998).

To address this limitation of using wing AR as a descriptor of wing shape, the present study additionally employed GM analysis to examine variation in wing shape across flying and perching behaviour and across flight heights of odonates. The results revealed no significant variation in wing shape between fliers and perchers.

The PCA plots revealed certain notable deviations in wing shape (see Figure 2). While *Crocothemis servilia* is classified as a percher, its forewing shape appears to be closely similar to *Pantala flavescens*, which is a typical flier. On the other hand, its hindwing shape deviates significantly away from all related libellulids considered in this study. This supports behavioural observations that *Crocothemis servilia* can switch flight behaviours, spending almost equal amounts of time perched and in flight, thereby deviating from the dichotomous classification of odonates into distinct behavioural types (Parr 1983; Corbet & May 2008).

*Tholymis tillarga* and *Gynacantha bayadera* are crepuscular dragonflies. *Tholymis tillarga*, which belongs to the family Libellulidae and is classified as a flier, is observed to have a forewing shape similar to other libellulid fliers such as *Pantala flavescens*, as expected. However, its hindwing shape appears to be closely similar to that of *Acisoma panorpoides*, a typical percher. This result supports observational records indicating that while *T. tillarga* exhibits rapid incessant flight during its crepuscular phase of peak activity, it tends to perch and rest among dense vegetation during the rest of the day (Miller & Miller 1985; Mitra 2005; Corbet & May 2008).

*Gynacantha bayadera*, which is an aeshnid and is classified as a flier, significantly deviates in its hindwing shape from that of *Anax guttatus*, which is also an aeshnid and a flier. This can be attributed to the difference in flight styles between the two aeshnids – *A. guttatus* tends to soar and fly at larger heights than *G. bayadera* (Miller 2007). Additionally, similar to the case of *T. tillarga*, observational studies have recorded *Gynacantha* spp. being inactive and perching under vegetation during mid-day hours and flying rapidly only during the active crepuscular phase (Clausnitzer 1999; Miller 2007).

Such deviations in wing shape being apparently associated with observable specialised behaviour, indicate that the dichotomous classification of odonates into perchers and fliers is too broad, possibly overlooking the nuanced flight patterns adopted by these insects. This demands a more comprehensive and detailed approach to understanding the flight patterns of odonates.

Wind speeds are known to influence the flight of insects, with greater heights experiencing greater wind speeds (Engels et al. 2016). Therefore, it can be hypothesized that odonates require adaptations in wing shape to optimize flight efficiency in accordance with their characteristic flight heights. Supporting this, our results revealed a significant variation in wing shape across flight heights. These results suggest that behavioural factors, especially flight heights may influence odonate wing shape, while also highlighting the importance of wing shape in flight efficiency. Consequently, the flight performance of biomimetic devices modelled after odonatan flight, can be enhanced by optimizing wing shape in accordance with the heights above ground at which these devices are intended to operate.

It is worth mentioning that the current study analysed a relatively small sample of 19 odonate species from the Hyderabad region. Although our results show significant correlations between wing shape and flight heights, and intriguing deviations in the wing shapes of some species,

the sample size may limit generalization of the results to all odonates. A more extensive study would be valuable by including a higher number of species from different geographical regions, belonging to various families and genera, for the validation of these findings. Such an increase in sampling might uncover further patterns in wing morphology and their relation to flight behaviour and height preference, thus bringing more robust information about the evolutionary history of odonate wing architecture.

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Mr. Jatishwor Singh Irungbam, Biology Centre CAS, Branišovská, Czech Republic.  
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Dr. Manju Siliwal, WILD, Coimbatore, Tamil Nadu, India  
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Dr. K.A. Subramanian, Zoological Survey of India, New Alipore, Kolkata, India  
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ravi@threatenedtaxa.org & ravi@zooreach.org

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