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Integrative taxonomic review of the genus *Peschetius* (Coleoptera, Dytiscidae, Hydroporinae) from India with description of two new species

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Abstract

The diving beetle genus *Peschetius* Guignot, 1942 (Coleoptera: Dytiscidae) in India is reviewed. Integrative taxonomic approach using morphology, multivariate morphometry and genetic analysis of cytochrome oxidase subunit 1 revealed the presence of four species, two of which are described here as new: *Peschetius bistroemi* **sp. nov.** from southern Western Ghats (Kerala) differs from all known congeners with distinctly broadened male antennomeres IV and V, shape of the prosternal process and the male genitalia; *P. nilssoni* **sp. nov.** from northern Western Ghats, Rajasthan and Madhya Pradesh is similar to the widespread Indian *P. toxophorus* Guignot, 1942, from which it differs in habitus, elytral colour pattern and the shape of the male genitalia. New records are presented for the remaining Indian species, namely *P. quadricostatus* (Aubé, 1838) and *P. toxophorus*. All species are diagnosed, illustrated and a key to their identification is provided.

Keywords

cryptic species, diving beetle, multivariate analysis, new species, species delimitation, Western Ghats

1. Introduction

The dytiscid genus *Peschetius* Guignot, 1942 includes ten species, out of which seven occur in Africa—south of the Sahara, and three in Asia (Biström and Nilsson 2003; Biström and Bergsten 2015; Nilsson and Hájek 2021). The genus is represented by three species from the Indian subcontinent: *Peschetius toxophorus* Guignot, 1942 is endemic to peninsular India while *P. quadricostatus* (Aubé, 1838) is widely distributed in India, and is also known from south-eastern Iran, Pakistan and Nepal (Hájek 2006; Ghosh and Nilsson 2012). The third species, *P. taproba-*

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nicus Biström and Bergsten, 2015, is endemic to Sri Lanka (Biström and Bergsten 2015).

Peschetius was proposed by Guignot (1935) to accommodate three previously described aberrant *Hydroporus*; later, Guignot (1942) formally made the genus name available by designating *P. nodieri* (Régimbart, 1895) as its type species. Due to the aberrant morphology, the genus *Peschetius* was traditionally included in the tribe Hydroporini of the eponymous subfamily. Guignot (1935) and Balfour-Browne (1946) both suggested its affinity with Australian genera *Antiporus* Sharp, 1882 and *Necterosoma* Macleay, 1871, currently classified within the subtribe Sternopriscina. However, Miller et al. (2006) revised the classification of Hydroporinae and proposed the genus *Peschetius* as a sister group to the members of the tribe Bidessini, chiefly based on presence of a prominent spermathecal spine, and the five-lobed teeth in the proventriculus. Therefore, the authors formally transferred *Peschetius* to the tribe Bidessini which is now widely accepted (see, e.g., Miller and Bergsten 2014).

African *Peschetius* were reviewed by Omer-Cooper (1970), while the two Indian species were diagnosed by Vazirani (1970a). Vazirani (1977c) discussed elytral pattern variability of *P. toxophorus*. The comprehensive, morphology-based, revision of the genus by Biström and Nilsson (2003) provided detailed species diagnoses and the first cladistic analysis of the genus.

While studying the systematics and morphology of dytiscid beetles from India, particularly Western Ghats, we have discovered four morphologically distinct species of *Peschetius*, for which species limits were also confirmed by a genetic analysis of mitochondrial cytochrome oxidase subunit 1 and by the analysis of morphometric data in an integrative way. The importance of combining traditional taxonomy and modern tools like DNA sequencing to unveil cryptic species has been currently highlighted e.g. by Dayrat (2005), Will (2005), Padial et al. (2010) and Schlick-Steiner et al. (2010). The delimitation of taxa using such an integrative approach, including the description of two new species is the main aim of the present paper.

2. Material and Methods

2.1. Study area

India is a major part of the Indian subcontinent which is flanked by the Himalayan mountains in the north, Arabian Sea in the west, Indian Ocean in the south and Bay of Bengal in the east (Fig. 1). The country has several physical features, such as Himalayas, Indo-Gangetic plains, central and eastern highlands, Thar desert, Gondwanan peninsular plateau, Western and Eastern Ghats and coastal plains. The Satpura range of mountains lies north of the peninsular plateau and forms a chief biogeographical barrier. The plateau gradually slopes down in the north via Madhya Pradesh to Indo-Gangetic plains in Uttar Pradesh, and in the northwest to Thar desert of Rajasthan. The western edge of this plateau is bordered by a chain of escarpments i.e. Western Ghats or Sahyadri range. The range passes through Gujarat, Maharashtra, Karnataka, Tamil Nadu and Kerala States of the country. The Ghats are interrupted by two biogeographic barriers, namely Palghat Gap and Shencottah Gap near Kerala (Fig. 1). The Palghat gap is flanked by Nilgiri range to the north and Annamalai hills to the south. The position of Himalayan orogen and afore-mentioned physical features of the Indian plate play a key role for the tropical monsoon as well as various climatic zones in India (Mani 1974).

2.2. Taxon sampling and specimen deposition

The beetles were captured using a pond net of mesh size 1 mm (EFE and GB Nets, Educational field equipment UK Limited; now https://www.nhbs.com/telescopic-pond-net) from the Western Ghats (Fig. 1) and were preserved in absolute ethanol. The alcohol was changed in laboratory and specimens were stored at –20°C for molecular work (Table 1). This material is deposited in the following collections:

HVGC Hemant Vasant Ghate Collection, Pune, India;
ICAR Indian Council of Agricultural Research, Bengaluru, India;
UASB University of Agricultural Sciences, Bengaluru, India;
ZSIP Zoological Survey of India, Western Regional Centre, Pune, India.

Additional material studied in this work was obtained from the following institutional and private collections:

BMNH Natural History Museum [former British Museum (Natural History)], London, United Kingdom;
HFCB Hans Fery collection, Berlin, Germany (property of NHMW);
JSCL Jaroslav Šťastný collection, Liberec, Czech Republic;
MNHN Muséum Nationale d'histoire Naturelle, Paris, France;
NHMW Naturhistorisches Museum Wien, Vienna, Austria;
NMPC Národní muzeum, Prague, Czech Republic;
ZSMG SNSB-Zoologische Staatssammlung München, Munich, Germany.

The distribution map of species was prepared using QGIS freeware (version 2.18.5; developer: Open-Source software; https://qgis.org/downloads). In addition to the material studied, the data for the map were also excerpted from the available literature (see under the respective species). The geographical coordinates of the localities were obtained using Google Earth Pro (https://www.google.com/intl/en_in/earth/versions). The details of examined specimens are listed in supplementary metadata file 1.

Table 1. Location and GenBank details for cytochrome oxidase subunit 1 gene sequences used in the study.

Tribe/Species	Location	Latitude	Longitude	GenBank	Reference
Peschetius bistroemi	India, Pala, Aimcombu	9°46′16″N	76°41′39″E	MW911323	Current study
Peschetius bistroemi	India, Pala, Aimcombu	9°46′16″N	76°41′39″E	MW911324	Current study
Peschetius bistroemi	India, Mukkada	9°28′7″N	76°47′43″E	MW911325	Current study
Peschetius bistroemi	India, Mukkada	9°28′7″N	76°47′43″E	MW911326	Current study
Peschetius nilssoni	India, Satara	17°39′44″N	73°58′5″E	MW911327	Current study
Peschetius nilssoni	India, Satara	17°39′44″N	73°58′5″E	MW911328	Current study
Peschetius nodieri	Ghana, Volta Region	8°31′12″N	0°36′11″E	KJ548542	Miller and Bergsten (2014)
Peschetius quadricostatus	India, Aimcombu	9°46′45″N	76°41′4″E	MW911329	Current study
Peschetius quadricostatus	India, Aimcombu	9°46′45″N	76°41′4″E	MW911330	Current study
Peschetius quadricostatus	India, Satara	17°40′58″N	73°58′21″E	MW911331	Current study
Peschetius quadricostatus	India, Satara	17°40′58″N	73°58′21″E	MW911332	Current study
Peschetius quadricostatus	India, Satara	17°40′58″N	73°58′21″E	MW911333	Current study
Peschetius quadricostatus	India, Maharashtra	16°34′60″N	73°35′14″E	KF575492	Miller et al. (2013)
Peschetius toxophorus	India, Satara	17°40′58″N	73°58′21″E	MW911334	Current study
Peschetius toxophorus	India, Satara	17°40′58″N	73°58′21″E	MW911335	Current study
Peschetius toxophorus	India, Chikmagalur	–	–	EF670065	Ribera et al. (2008)
Amarodytes sp.	Peru, Madre de Dios	12°50′12″S	69°17′36″W	KF575474	Miller et al. (2013)

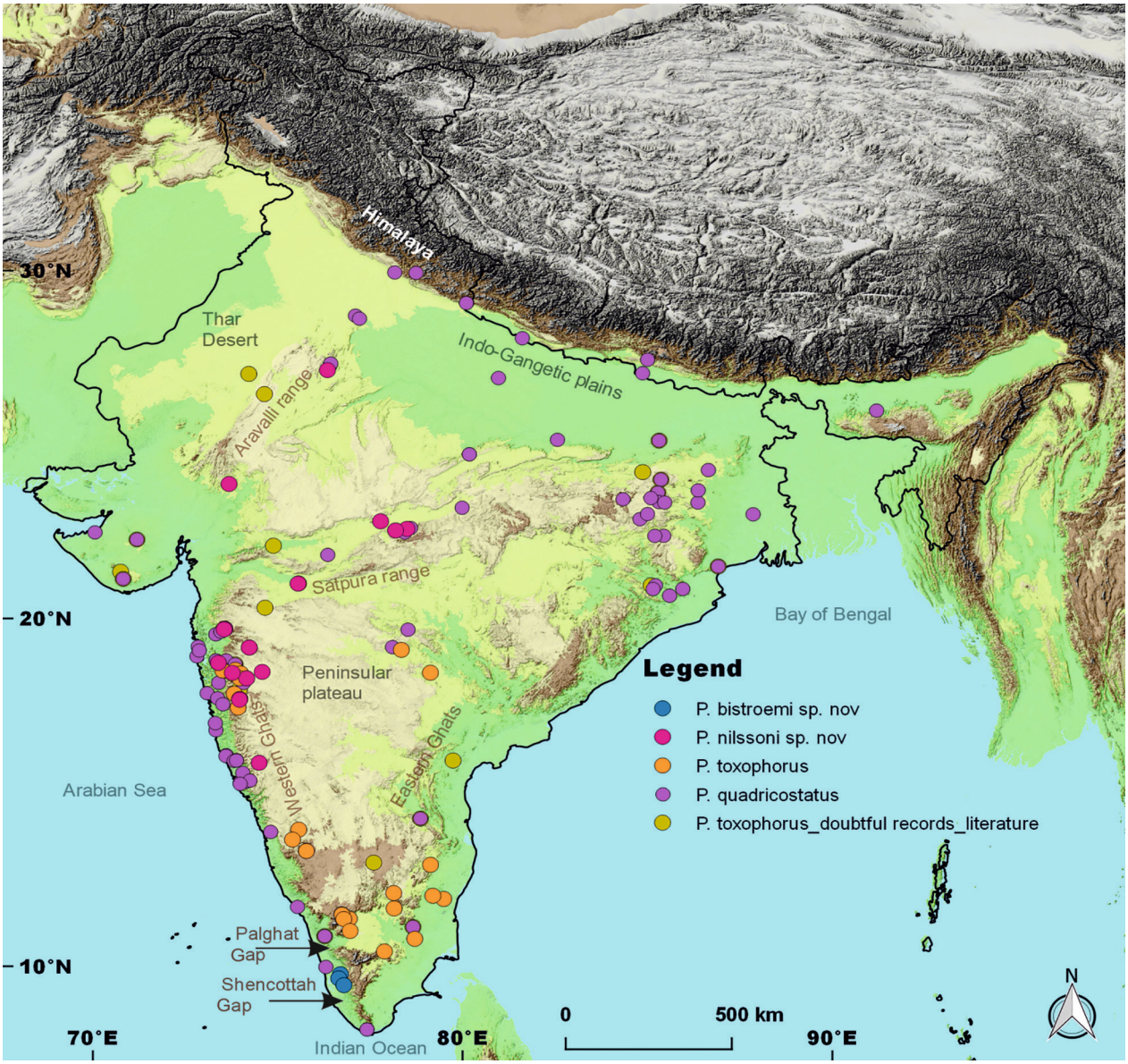

Figure 1. Distribution of *Peschetius* species along the main geographical features of India.

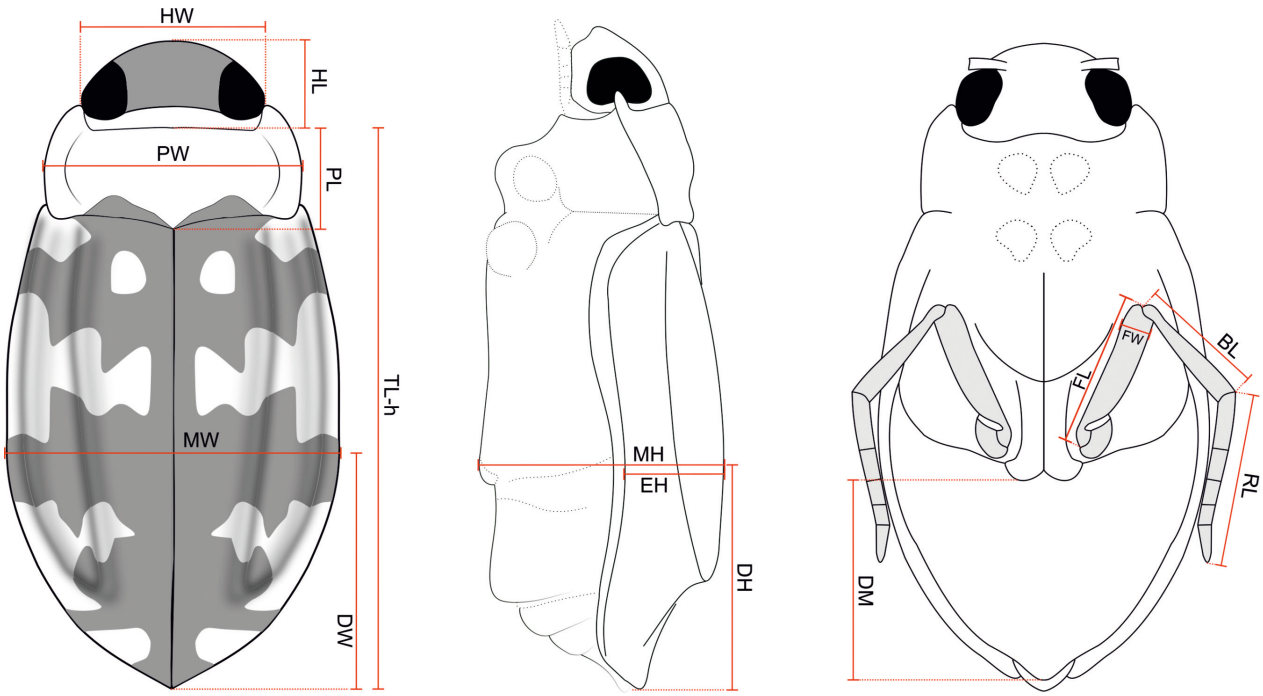

Figure 2. Diagrammatic representation of measurements taken for multivariate morphometric analysis (lateral view adapted from Miller et al. 2006). Abbreviations: **TL-h** Length of anterior border of pronotum to tip of elytra **MW** maximum width of body **HL** length from clypeal border to posterior side between eyes **HW** maximum width across eyes **PL** median length of pronotum **PW** maximum width of pronotum **DW** distance between level of maximum width to tip of elytra **DM** distance between end of metacoxae to tip of elytra **FL** length of metafemur **FW** width of metafemur **BL** length of metatibia **RL** length of metatarsus **EH** maximum length of elytra (lateral) **MH** maximum height of body (lateral) **DH** distance between level of maximum height to tip of elytra.

2.3. Morphological study and illustrations

Measurements were taken with an ocular micrometre. The following abbreviations were used in the descriptions: **TL** – total length of body, a single measurement of length from front of head to apex of elytra; **TL-h** – total length without head length, length of body from anterior margin of pronotum to apex of elytra; **MW** – maximum width of body. Miller and Nilsson (2003) was followed for the terminology to denote the orientation of the genitalia.

Digital images of habitus and male genitalia were prepared as described by Sheth et al. (2021). Additionally, the specimens were studied under Nikon SMZ800 and photographed under Nikon SMZ25 and Nikon SMZ1270, both with NIS elements D software (version 5.01.00 and version 5.20.00, respectively; Nikon Corporation; https://www.nikon.com). For the study of female genitalia, the female specimens were treated using 10% KOH for 24 hours. The spermathecae were dissected out in a water drop under Nikon SMZ800 and photographed in glycerine jelly using Olympus BX3+Olympus DP3+Olympus U-CMAD3 T7 assembly with CellSens dimension software (version 1.16; Olympus Corporation; https://www.olympus-lifescience.com/en). The photographs were stacked using Helicon-Focus software (version 5.1.19; Helicon Software Limited; https://www.heliconsoft.com). The photographs of habitats of new species were captured using Google Pixel phone (model 3a; Appendix 1).

2.4. Morphometry and morphometric analysis

Fifteen morphological characters were measured using a Lawrence and Mayo stereo zoom microscope fitted with an ocular micrometre for 58 adult beetles. The abbreviations and full names of characters are as follows (Fig. 2; see also Ribera and Nilsson 1995):

TL-h – body length, **MW** – maximum width, **HL** – length from clypeal border to posterior side between eyes, **HW** – maximum width across eyes, **PL** – median length of pronotum, **PW** – maximum width of pronotum, **DW** – distance between level of maximum width to tip of elytra, **DM** – distance between end of metacoxae to tip of elytra, **FL** – length of metafemur, **FW** – width of metafemur, **BL** – length of metatibia, **RL** – length of metatarsus, **EH** – maximum length of elytra; lateral, **MH** – maximum height of body; lateral, and **DH** – distance between level of maximum height to tip of elytra.

Between-group Principal Component Analysis (bgPCA) on raw morphometric data was performed. To account for scale difference among characters, bgPCA on correlation matrix was performed. Since in bgPCA, the eigenanalysis is carried out on the group means (Krzanowski 1979), it extracts fewer principal components that explain most of the variation in the data; as a result, low dimensional PCA plot is reliable for understanding most of the variation in high dimensional multivariate data. Because bg-

PCA can suffer from certain limitations (Cardini et al. 2019), the significant differences between groups were independently tested using Permutations Multivariate Analysis of Variance (PERMANOVA) (Anderson 2001). PERMANOVA tests the null hypothesis that the centroids and dispersion of the groups are equivalent for all groups. PERMANOVA was performed using Euclidian distance and 9999 permutations. Overall PERMANOVA was performed to check whether at least one of the group centroids was different. If overall PERMANOVA was significant, then significant differences between pairs of groups were tested using pairwise PERMANOVA. Since multiple tests were performed on the same data, family wise error rate was controlled using sequential Bonferroni correction. All statistical analysis was performed in the software PAST (version 4.02; Hammer et al. 2001).

2.5. Molecular analysis

The DNA was extracted from whole individuals using a QIAamp DNA Mini Kit (Qiagen, Hilden, Germany, Catalog No. 51306) following the manufacturer's protocol. Partial sequence of mitochondrial cytochrome oxidase subunit 1 (*cox1*) was amplified using the primer pair Jerry (5'-CAA CAT TTA TTT TGA TTT TTT GG-3') and M70 (5'-TTC ATT GCA CTA ATC TGC CAT ATT A-3') with an annealing temperature of 57°C (Simon et al. 1994; Lunt et al. 1996). PCR amplification, PCR product purification and sequencing protocols were done according to Suranse et al. (2017). Molecular sequence data generated for the present work are deposited in the GenBank database. Please refer to Table 1 for details of sequences generated in this study and other sequences obtained from the GenBank database. *Amarodytes* sp. (KF575474) was used as an outgroup following its sister taxa relationship provided by Miller et al. (2013).

Sequences were aligned in MEGA (version 7; Kumar et al. 2016) using MUSCLE (Edgar 2004). Pairwise raw genetic distances were estimated using MEGA 7 (Kumar et al. 2016). Data were partitioned by the three codon positions of the *cox1* gene. Partition analysis (Chernomor et al. 2016) and ModelFinder (Kalyaanamoorthy et al. 2017) were used to find the optimal partitioning scheme with the best-fitting nucleotide substitution model for each partition selected by the minimum Bayesian Information Criterion (BIC) (Schwarz 1978). A maximum likelihood (ML) analysis was conducted using IQ-TREE (version 1.6.12; Nguyen et al. 2015) on the partitioned dataset using the proposed models with topological support inferred by 1000 iterations of ultrafast bootstrapping (Hoang et al. 2018). The resulting phylogenetic tree was edited in FigTree (version 1.4.2; Rambaut 2009).

We performed genetic species delimitation using two methods. Assemble species by automatic partitioning (ASAP) delimits species based on genetic gap analysis (Puillandre et al. 2021). ASAP was performed online (https://bioinfo.mnhn.fr/abi/public/asap/) using genetic uncorrected p distances. General mixed Yule-Coalescent (GMYC) method is a likelihood- based method for delimiting species by fitting within- and between-species branching models to reconstructed gene trees (Fujisawa and Barraclough 2013). GMYC was performed online (https://species.h-its.org/gmyc/) using single threshold and ultrametric Bayesian tree as an input. The Bayesian ultrametric tree was generated using Markov Chain Monte Carlo (MCMC) analysis implemented in BEAST v1.8.4 (Drummond et al. 2012) with strict clock and two runs of 10 million generations (sampling trees every 1,000 generations and first 10% trees were discarded as burnin).

3. Results

3.1. Morphometric analysis

Between-group PCA extracted three components which explained all the variation in the data. The specimens of Indian *Peschetius* grouped under four separate clusters in the PCA (Fig. 3A). The null hypothesis that all the clusters were the same was rejected (PERMANOVA, F = 33.93, p = .0001) (Fig. 3B), suggesting that the centroid of at least one of the clusters was significantly different. Pairwise comparison of clusters revealed that all the clusters were significantly different from each other, even after sequential Bonferroni correction (Fig. 3C). Thus, this analysis clearly indicated that there are four *Peschetius* morphospecies occurring in India.

3.2. Molecular analysis

ModelFinder identified two partitions, one comprising the combined first and second codon positions, and other comprising third codon position of *cox1* gene. Nucleotide substitution models for the partitions were TIM2+F+R2 and HKY+F+G4, respectively. The maximum likelihood analysis placed the specimens of Indian *Peschetius* into four well-supported clades (Fig. 4). *Peschetius nilssoni* sp. nov. was recovered convincingly as the sister species to *P. toxophorus* (ultrafast bootstrap support, UFB = 96). *Peschetius bistroemi* was recovered as being more distantly related to the other Indian species which are together placed in a clade, albeit with weak support (UFB = 68). Maximum intra-species raw genetic distance among Indian *Peschetius* species was 1.0 % while the minimum inter-species genetic divergence was 2.7 % (Table 2). *Peschetius nilssoni* sp. nov. differed from all its congeners, for which the genetic data are available, with a raw genetic distance of 2.7–14.3%, while *P. bistroemi* sp. nov. differed from other congeners with a raw genetic distance of 12.7–14.3%.

Both species delimitation methods, ASAP and GMYC, indicated four distict species of *Peschetius* from Indian subcontinent (Fig. 4). The best partition of ASAP had the highest relative gap width metric W of 0.00372 and threshold distance of 1.8% and identified *Peschetius nils-*

Table 2. Minimum and maximum percentage raw genetic distances between species of *Peschetius*.

Species		[1]	[2]	[3]	[4]	[5]
Peschetius bistroemi (4 spec.)	[1]	0.5–1.0				
Peschetius nilssoni (2 spec.)	[2]	13.2–14.3	**1**			
Peschetius nodieri (1 spec.)	[3]	13.5–13.7	13.2–14.3	–		
Peschetius quadricostatus (6 spec.)	[4]	12.8–13.6	10.6–11.2	12.8–13.3	**0.1–0.8**	
Peschetius toxophorus (3 spec.)	[5]	12.7–13.7	2.7–3.3	12.7–12.8	10.7–11.4	**0.0–0.1**

Note: Values in bold are intraspecific distances. The number placed after species name indicates number of sequences used per species in the analysis.

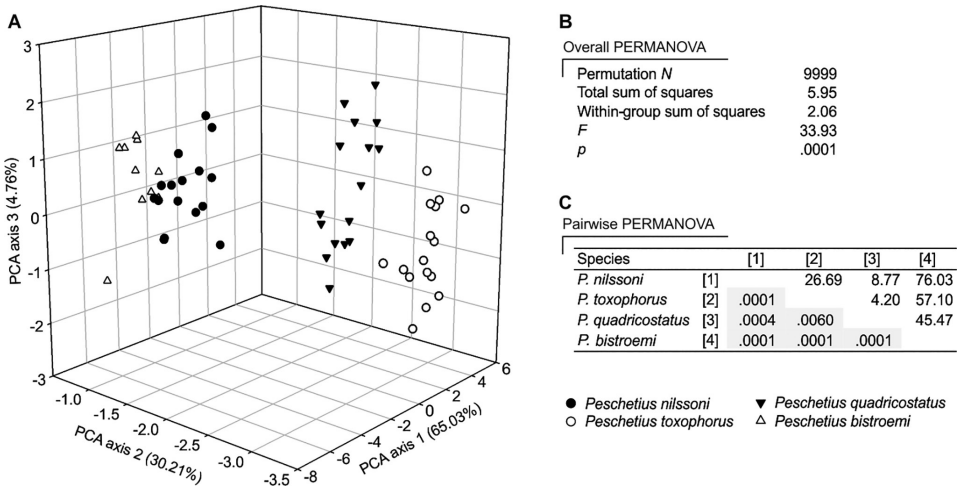

Figure 3. Multivariate analysis of morphometric data of four Indian species of *Peschetius*. **A** Scatter plot of factor scores of between-group PCA (values in parenthesis are percentage variation explained by each PCA axis) **B** Overall PERMANOVA indicated that at least one of the species has significantly different centroid **C** Pairwise PERMANOVA between species suggested that all species are morphometrically significantly different even after sequential Bonferroni correction (the *F* values are provided above diagonal and *p* values are provided below diagonal in grey cells).

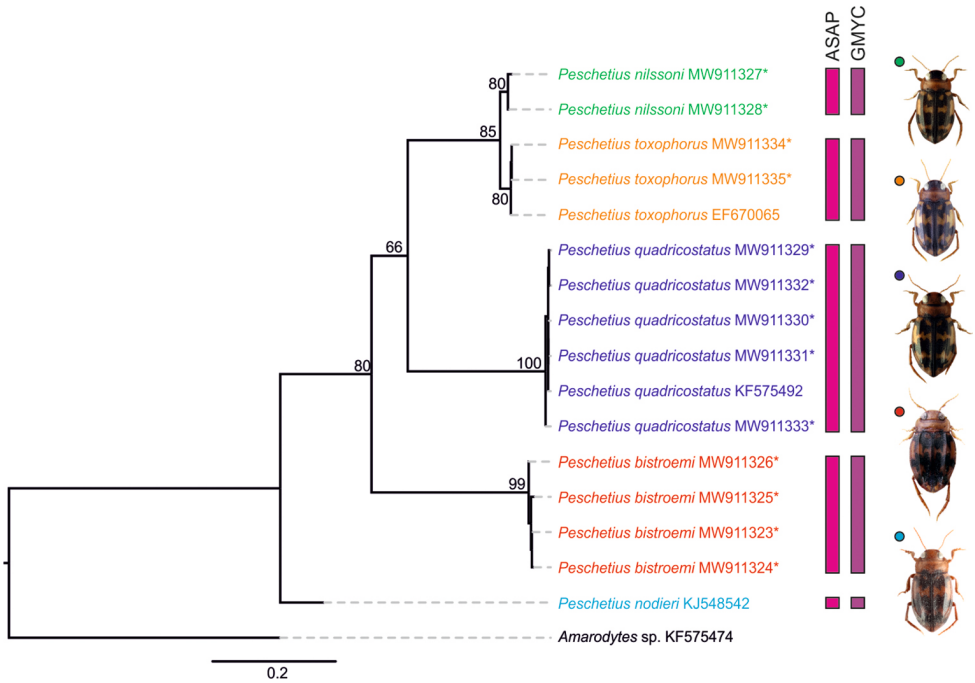

Figure 4. Maximum likelihood tree of the genus *Peschetius*. The analysis was based on mitochondrial cytochrome oxidase subunit 1 partial sequences employing best partition scheme and nucleotide substitution model (log-likelihood of consensus tree = -2209.079). *Amarodytes* sp. is used as an outgroup. Values along the nodes are percentage bootstraps out of 1000 iteration. *Peschetius* species delimitation based on assemble species by automatic partitioning (ASAP) and general mixed Yule-Coalescent model (GMYC) are shown by bars next to species names. Sequences with asterisk are generated in the current study.

soni sp. nov. and its sister taxa *P. toxophorus* as distinct species (Supplementary file 2). Similarly, GMYC identified six distinct maximum likelihood entities (likelihood ratio test, P = 0.0015) for four Indian species of *Peschetius*, one African species of *Peschetius* and the outgroup (Supplementary file 3).

3.3. Taxonomy

Peschetius Guignot, 1942

Type species. *Hydroporus nodieri* Régimbart, 1895, by original designation.

Diagnosis. Body length 2.95–4.35 mm. Dorsal aspect of body with distinct colour pattern; body outline discontinuous with distinct angle between pronotum and elytra; elytral surface strongly bicarinate; elytral epipleuron broad, base of epipleuron not delimited by a transverse carina; metacoxal lines raised, with region between them deeply foveate; abdomen tectiform, basally in the middle (close to metatrochanters) with wide depression; basal ventrites with a variable number of wide 'macropunctures' (Biström and Nilsson 2003; Miller et al. 2006). The species under this genus are externally rather homogeneous but the shape of the prosternal process and male genitalia are diagnostic (Biström and Nilsson 2003).

3.3.1. *Peschetius bistroemi* sp. nov.

Figs 5A, 6A, 7A, 8A

http://zoobank.org/ED915A59-725D-4A22-8E67-6BCC386-6638

Specimens examined. Holotype: INDIA • ♂; Kerala, Kottayam district, Pambady; 9°35′21″N, 76°34′59″E; ca 10 m.a.s.l.; 7 Jan. 2020; S. D. Sheth leg.; streamlet; Indian Council of Agricultural Research, Bengaluru, India [ICAR]. **Paratypes:** INDIA – **Kerala** • 1 ♀; same data as holotype; ZSIP • 1 ♂, 1 ♀; Mukkada; 9°28′7″N, 76°47′43″E; ca 100 m.a.s.l.; 7 Jan. 2020; S. D. Sheth leg.; streamlet; UASB • 1 ♂; Aimcombu; 9°46′16″N, 76°41′39″E; ca 50 m.a.s.l.; 7 Jan. 2020; S. D. Sheth leg.; streamlet; HVGC.

Description of male holotype. ***Habitus*:** Body elongate, widest before midlength of elytra; lateral outline of body discontinuous with distinct angle between pronotum and elytra; elytral keels prominent (Fig. 5A). — ***Colouration*:** Head ferruginous. Appendages testaceous. Pronotum ferruginous, with bilobed black band near posterior margin. Elytron blackish with typical testaceous markings consisting of two subbasal spots, premedian and postmedian transverse bands, and preapical spot; testaceous spot near humeral angle of elytra reduced. Ventral side overall testaceous. Prosternum darker along anterior margin, prosternal process with black border. Metaventrite darker apically, posterior margins of abdominal ventrites darkened. Coxae ferruginous. — ***Head*:** Transverse (broader than long), eyes slightly emarginate. Antennae with antennomeres IV and V markedly globular and swollen, ventrally flat; antennomeres VI and VII broader, ventrally flat. Width across eyes is 2X the width between eyes. Clypeus arcuate. Labrum emarginate with series of setae on anterior margin. Punctation of head dense, distance between punctures smaller than puncture diameter. Punctures fine on clypeus, becoming progressively coarser posteriorly on frons, occipital part posterior to eyes impunctate. Setiferous punctures present in well-developed fronto-clypeal depressions and as a row along inner margin of eyes. Reticulation consisting of polygonal, slightly transverse meshes on clypeus; posterior part of frons smooth. Impunctate occipital part posterior to eyes distinctly microreticulate. — ***Pronotum*:** Transverse. Anterior margin straight, sides almost straight, curved anteriorly, posterior margin gently sinuate; anterior corners acute, posterior margins obtuse. Pronotal disc with posterior depression prominent. Pronotum with distinct depressions between disc and sides, mediolaterally between disc and posterior margin. Pronotal disc strongly vaulted. Punctation dense, distances between punctures smaller than puncture diameter. Punctures setiferous, finer on disc, becoming coarser on margin and sides. Surface between punctures microreticulate with shallowly impressed polygonal meshes visible on either side of disc. — ***Elytra*:** Widest before midlength, keels prominent. Punctation of elytra coarser than on head and pronotum. Punctation dense, distance between punctures smaller than puncture diameter. Punctures finer along suture, costae and lateral margin, coarser on disc. Surface between punctures microreticulate with well impressed polygonal meshes. — ***Legs*:** Tibiae club-shaped, dorsally with long natatorial setae; pro- and mesotarsi broadened, dorsally with long natatorial setae, ventrally with adhesive setae; metatarsi with long natatorial setae on both sides. — ***Ventral side*:** Prosternum sinuate on anterior margin, portion between procoxae narrowed. Prosternal process broad anteriorly, narrowed posteriorly, without transverse depression and without keel but slightly raised (Fig. 7A). Mesoventrite bifurcated on anterior margin, posterior margin rounded. Metaventrite with coarse punctures, distance between punctures almost equal or larger than puncture diameter. Surface microreticulate with shallowly impressed polygonal meshes. Anterior border of metaventrite with two shallow but distinct depressions below mesocoxae. Metacoxal plate with coarse punctures. Distance between punctures smaller than puncture diameter. Reticulation similar to that of metaventrite. Metacoxal process raised. Abdomen with five ventrites (V1 to V5); V1 with 6–10 while V2 with 2–5 macropunctures arranged in two rows on either side. V2 to V5 covered with setigerous punctures; V3 to V5 with distinct lateral depression; depression on V3 less prominent; reticulation of V2 to V5 consists of polygonal meshes. Punctures on ventral surface setiferous. — ***Male genitalia*:** Median lobe broad at base and narrowed towards apex, gently curved, and with a basal process

(Fig. 6Aa). Parameres with long setae in apical half, apex rounded (Fig. 6Ab).

FEMALE. As male but antennomeres simple, not modified. Pro- and mesotarsi slender or less broadened. Spermatheca as in (Fig. 8A)—spermathecal spine long and slender.

Measurements (*N*=10). Body length 2.95–3.20 mm (holotype: 3.04 mm) and maximum width 1.65–1.85 mm (holotype: 1.72 mm). See also Supplementary file 4.

Variability. The specimens of type series are uniform with slight variation in elytral maculation.

Differential diagnosis. *Peschetius bistroemi* sp. nov. is easily recognised from all known *Peschetius* species based on distinctly broadened antennomeres IV and V in males—a character unique within the genus *Peschetius*. With nearly a flat prosternal process (i.e. without transverse depression or longitudinal keel), the new species is similar and probably related to *P. taprobanicus* from Sri Lanka; however, it differs from the latter species in the shape of male genitalia: the apex of median lobe is not bent as in *P. taprobanicus* and the curvature of the median lobe of *P. bistroemi* sp. nov. is shallower. The parameres of *P. bistroemi* sp. nov. are abruptly narrowed and rounded at their apex while in *P. taprobanicus* those are gradually narrowed. The setae of the parameres are present in the apical half in *P. bistroemi* sp. nov. while in *P. taprobanicus* these are restricted to the apex. Further, the spermathecal spine in *P. bistroemi* sp. nov. is longer than the other three Indian species, and not curved like that in *P. nilssoni* sp. nov.

Etymology. The species is named in the honour of Prof. Olof Biström (Helsinki, Finland) for his significant contribution to the taxonomy of Dytiscidae, including the genus *Peschetius*. The name is a noun in the genitive case.

Collection circumstances. The specimens were found in slow flowing streamlets with rock and mud as substratum, and decaying leaves.

Distribution. The species is so far known only from three close localities in Kottayam district, Kerala, southwestern India.

3.3.2. *Peschetius nilssoni* sp. nov.

Figs 5B, 6B, 7B, 8B

http://zoobank.org/304A1A89-C68F-45ED-9C9B-01E7AA1E-250B

Peschetius andrewesi Balfour-Browne 1946: 104 (partim.)
Peschetius toxophorus: Vazirani 1977c: 126 (partim.)

Specimens examined. Holotype: INDIA • ♂; Maharashtra, Pune, Ane; 19°09′47″N, 74°14′4″E; 800 m a.s.l.; 15 Sep. 2016; S. D. Sheth leg; pond; Indian Council of Agricultural Research, Bengaluru, India [ICAR]. **Paratypes:** INDIA – **Maharashtra** • 3 ♂♂, 3 ♀♀; same data as holotype; UASB • 1 ♂, 1 ♀; Pune, Jejuri; 18°16′39″N, 74°9′22″E; ca 750 m.a.s.l.; 22 Feb. 2014; S. D. Sheth leg.; reservoir; HVGC • 1 ♀, Nashik, Igatpuri, 19°42′13″N, 73°34′30″E, ca 600 m.a.s.l., 17 Jan. 2014, S. D. Sheth leg.; reservoir; ZSIP • 1 ♀; Pune, Talegaon; 18°42′58″N, 73°41′18″E; ca 600 m.a.s.l.; 16 Feb. 2014; reservoir; S. D. Sheth leg.; ZSIP • 1 ♀; Pune, Panshet; 18°22′57″N, 73°37′17″E; ca 600 m.a.s.l.; 7 June 2014; S. D. Sheth leg.; pond; HVGC • 1 ♂; Satara, Mahardara; 17°40′59″N 73°58′23″E; ca 750 m.a.s.l.; 16 Jul. 2014; S. D. Sheth leg.; pond; HVGC • 2 ♂♂; 120 km NE of Mumbai, Igatpuri env.; 19°42.17′N 73°33.06′E [19°42′11″N, 73°33′4″E]; ca 600 m.a.s.l.; 1 Aug.–12 Aug. 2002; P. Šípek and M. Fikáček leg.; NMPC • 1 spec.; 4 km S of Lonavala, Bushi [Bhushi] dam env.; [18°42′8″N, 73°25′3″E]; 500 [ca 600] m.a.s.l.; 12 Oct.–15 Oct. 2005; J. Bezděk leg.; NMPC • 1 ♂; Western Ghats Mts., Amboli env., 50 km W Belgaum, Daudki; [15°51′4″N, 74°29′52″E]; [ca 800 m.a.s.l.]; 21 May–23 May 2006; V. Ryjáček leg.; drying up river; NMPC. – **Rajasthan** • 1 ♀; Alwar di., Naranimata env.; 27°08′22″E 76°20′38 [27°8′21″N, 76°20′39″E]; 460 [ca 450] m.a.s.l.; 6.-7.2002; P. Šrámek leg.; NMPC • 1 ♂; NW of DUNGARPUR; 23°52′N 73°41′E [23°51′60″N, 73°40′60″E]; ca 250 m.a.s.l.; 1 Jul.–2 Jul. 2006; Z. Kejval leg.; along river; NMPC. **Other material:** INDIA – **Madhya Pradesh** • 3 ♀♀; Hoshangabad Dist., Bandrabhan, ca. 60 km SSE Bhopal, ca. 5 km NE Hoshangabad, Riv. Narmada; 22°47′29″N, 77°46′50″E; ca 280 [ca 300] m.a.s.l.; 23 Feb.–24 Feb. 2008; M. Jäch, S and P Sharma leg.; NHMW • 1 ♀; Hoshangabad Dist., River Denwa, ca. 8 km SSE Matkuli, Satpura range; 22°34′29″N, 78°29′43″E; ca 400 m.a.s.l.; 28 Feb. 2008; M.Jäch S and P Sharma leg.; NHMW • 1 ♀; Hoshangabad Dist., Sona, Bhadra [stream], northern part of Satpura NP, head of River, Denwa, Reservoir, Satpura Range, Lagdha Beta; 22°31′38″N, 78°11′18″E; 365 [ca 350] m.a.s.l.; 29 Feb. 2008; M.Jäch, S and P Sharma leg.; NHMW. – **Maharashtra** • 3 spec.; Khandesh; [20°59′60″N, 75°32′60″E]; [229 m.a.s.l.]; T.R. Bell leg.; BMNH [paratypes of *P. andrewesi*] • 1 ♀; Igatpuri; [19°40′60″N, 73°32′60″E]; 2000ft [ca 600 m.a.s.l.]; H.L. Andrewes leg.; BMNH [paratype of *P. andrewesi*].

The specimens listed in other material agree well with the type material of *P. nilssoni* but in absence of the male, we prefer not to designate them as paratypes.

Description of male holotype. *Habitus*: Body elongate, oblong oval, widest before midlength of elytra; outline discontinuous with distinct angle between pronotum and elytra; elytral keels prominent; dorsal surface submatt (Fig. 5B). — ***Colouration*:** Head black except testaceous occipital part posterior to eyes, appendages testaceous. Pronotum testaceous with bilobed black band near posterior margin extending to posterior corners. Elytron blackish with typical testaceous markings consisting of two subbasal spots, two premedian spots, postmedian transverse band and preapical spot. Ventral side overall ferruginous. Prosternum darker along anterior margin, prosternal process with black border. Posterior margins of abdominal ventrites dark. Legs testaceous. — ***Head*:** transverse, eyes slightly emarginate. Antennae with all antennomeres slender, club-shaped. Width across eyes 1.8X the width between eyes. Clypeus arcuate. Labrum deeply emarginate with series of setae on anterior margin. Punctation of head dense, distance between punctures smaller than puncture diameter. Punctures fine on

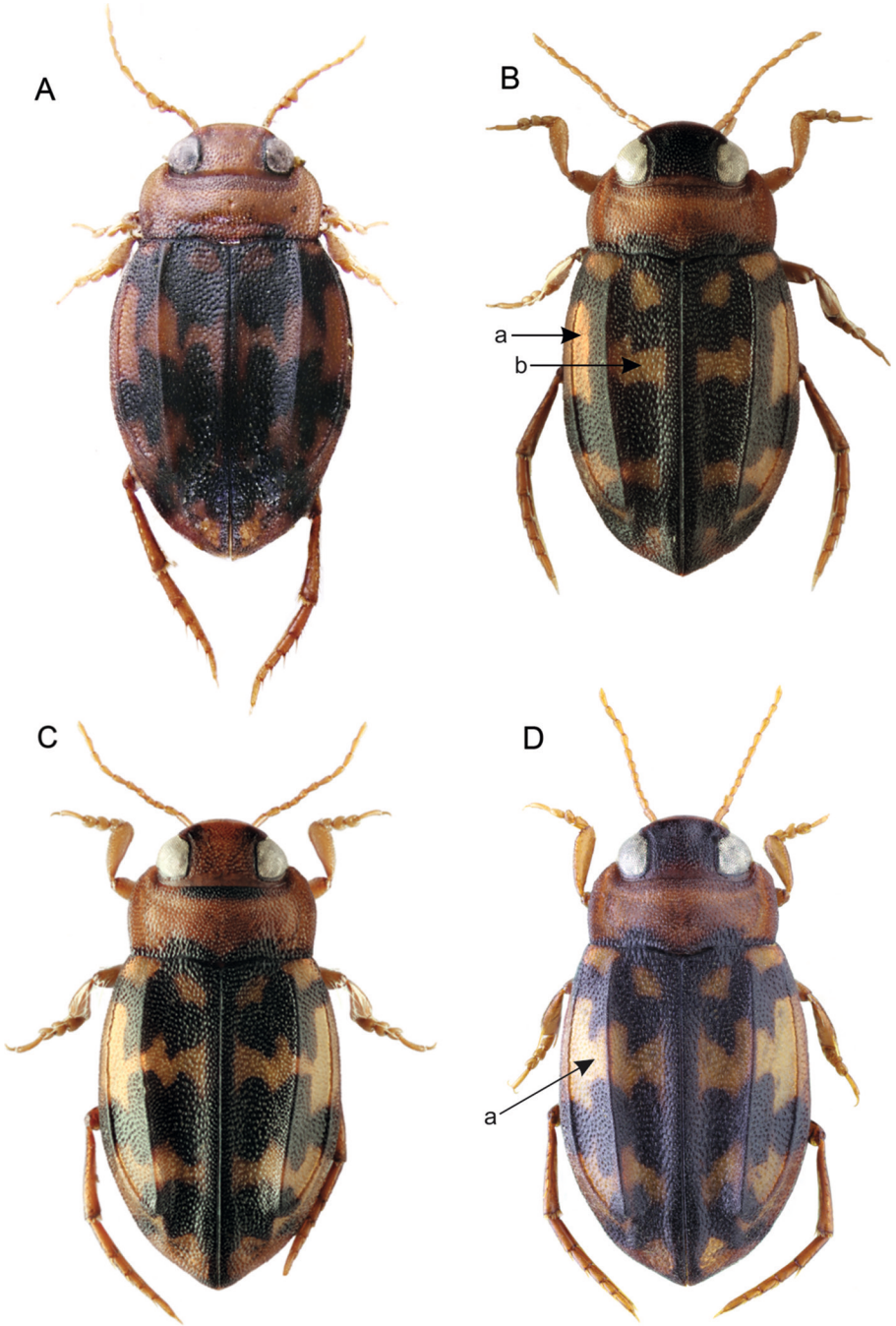

Figure 5. Dorsal habitus of Indian *Peschetius*. **A** *P. bistroemi* sp. nov. (Holotype) **B** *P. nilssoni* sp. nov. (Paratype—**a** longitudinal spot, **b** transverse spot; Amboli, Maharashtra) **C** *P. quadricostatus* (Amboli, Maharashtra) **D** *P. toxophorus* (**a** uninterrupted transverse band; Kotagiri, Tamil Nadu). (Body length: **A** 3.04 mm, **B** 3.15 mm, **C** 3.40 mm, **D** 3.35 mm).

clypeus, becoming progressively coarser posteriorly on frons, occipital part posterior to eyes impunctate. Setiferous punctures present in well-developed fronto-clypeal depressions and as a row along inner margin of eyes. Reticulation consisting of polygonal, slightly transverse meshes present on clypeus and in anterior part on frons; posterior part of frons smooth. Impunctate occipital part coarsely microreticulate. — ***Pronotum*:** Transverse. Anterior margin straight, sides evenly rounded, posterior margin gently sinuate; anterior corners acute, posterior angles obtuse. Pronotum with distinct depressions between disc and sides, mediolaterally between disc and posterior margin. Pronotal disc strongly vaulted. Punctation dense, distances between punctures smaller than puncture diameter. Punctures setiferous, finer on disc, becoming coarser on margin and sides. Surface between punctures microreticulate with shallowly impressed, polygonal meshes. — ***Elytra*:** Widest before midlength, keels prominent. Punctation dense, distance between punctures approximately equal to puncture diameter. Punctures finer along suture, costae and lateral margin, coarser on disc. Surface between punctures microreticulate, reticulation similar to that of pronotum. — ***Legs*:** Tibiae club-shaped, dorsally with long natatorial setae; pro- and mesotarsi broadened, dorsally with long natatorial setae, ventrally with adhesive setae; metatarsi with

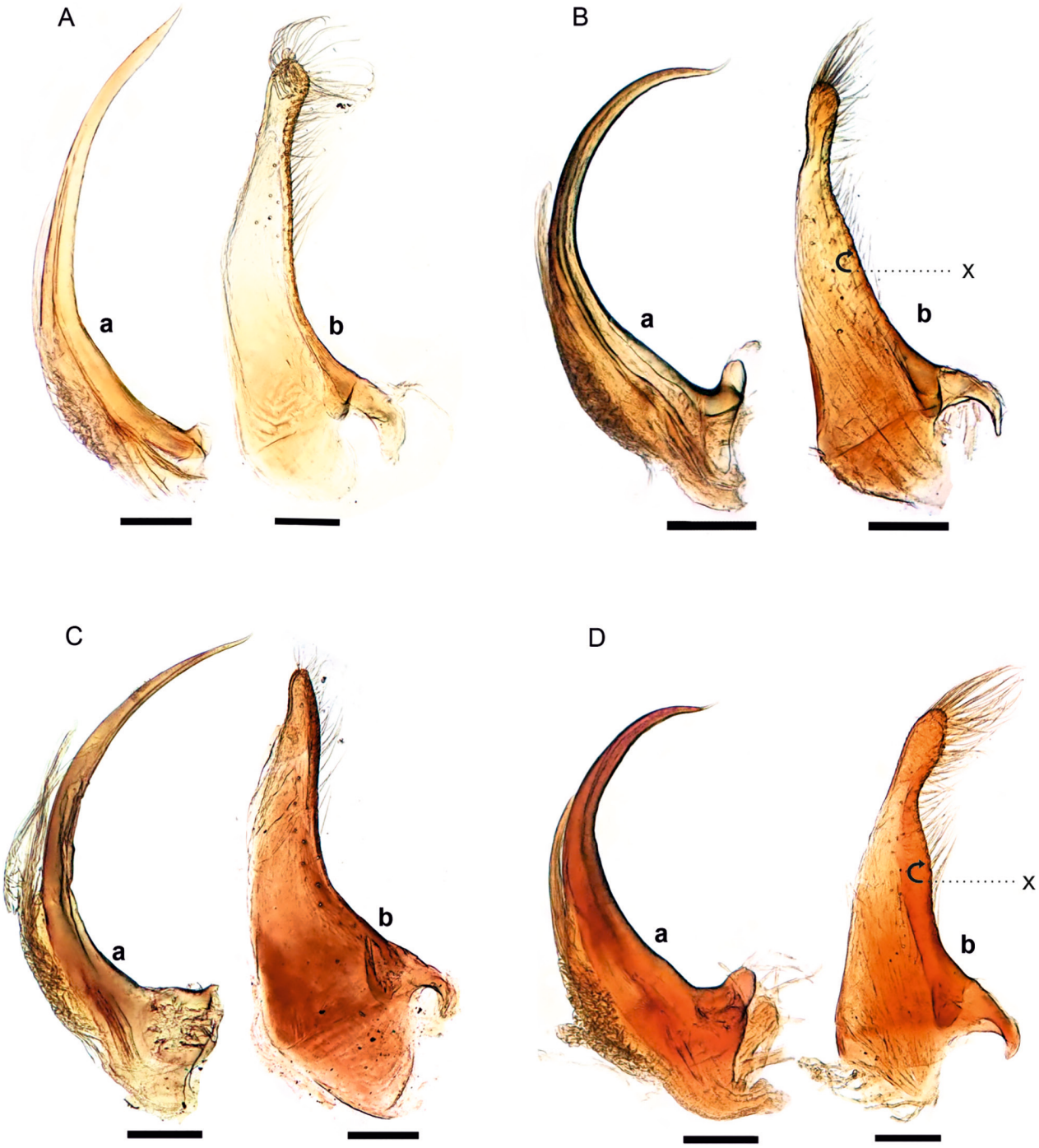

Figure 6. Male genitalia of Indian *Peschetius* (a. median lobe; b. paramere; bx. tapering of paramere). **A** *P. bistroemi* sp. nov. (holotype) **B** *P. nilssoni* sp. nov. (holotype) **C** *P. quadricostatus* (Jejuri, Maharashtra) **D** *P. toxophorus* (Satara, Maharashtra). Scale bars: 100 µm (**A, B, C, D**).

long natatorial setae on both sides. — ***Ventral side*:** Prosternum sinuate on anterior margin, area between procoxae narrowed. Prosternal process elongate, flat basally, laterally compressed posteriorly, convex with short keel apically, apex tuberculate, posteriorly narrowed, without transverse depression (Fig. 7B). Mesoventrite bifurcated on anterior margin, posterior margin rounded. Metaventrite densely punctate with coarse punctures, distance between puncture approximately equal to puncture diameter. Surface microreticulate with shallowly impressed polygonal meshes. Anterior border of metaventrite with two prominent depressions below mesocoxae. Metacoxal plate with punctation and reticulation similar to that of metaventrite. Metacoxal lines raised. Abdomen with five ventrites (V1 to V5); V1 with 8–10 macropunctures in one row and V2 with 8–10 macropunctures in two rows on either side; punctures on V2 prominent while those on V3 to V5 shallow; V3 to V5 with lateral depression shallow; V3 longitudinally obtusely keeled; reticulation of V2 to V5 consists of polygonal meshes. Punctures on ventral surface setiferous.— ***Male genitalia*:** Median lobe broad at base, narrowed towards apex, evenly

curved or 'C' shaped, and with basal process (Fig. 6Ba). Parameres with extended setae in apical half, apex rounded (Fig. 6Bb).

FEMALE. Identical to male in habitus, dorsal surface reticulation more impressed, thus beetles appearing matt. Apex of prosternal process non-tuberculate. Pro- and mesotarsi less broadened. Spermatheca as in (Fig. 8B)—spermathecal spine curved.

Measurements (*N*=22). Body length 2.60–3.15 mm (holotype: 2.75 mm), and maximum width 1.64–1.74 mm (holotype: 1.64 mm). See also Supplementary file 4.

Variability. The species slightly varies in body size and width. The shape of sub-basal yellow spot on elytra varies within species.

Differential diagnosis. With the black head, and the prosternal process convex with a short apical keel, and the general shape of the male genitalia, *Peschetius nilssoni* sp. nov. is very similar and undoubtedly closely related to *P. toxophorus*. This fact is confirmed also by the raw genetic distance as measured by the *cox1* gene, which is 2.7–3.3%—the least differentiated within Indian *Peschetius*. The two species can be easily recognised based on the shape of the testaceous premedian transverse band on elytra, which is always interrupted between elytral costae in *P. nilssoni* sp. nov. forming lateral longitudinal spot (Fig. 5Ba) and discal transverse spot (Fig. 5Bb) while the band is always uninterrupted in *P. toxophorus* (Fig. 5Da). Additionally, the body shape of *P. nilssoni* sp. nov. is more elongate and narrower (Fig. 5B), while it is broader in *P. toxophorus* (Fig. 5D). These differences in body shape were also confirmed with the multivariate morphometric analysis (Fig. 3). Further, the median lobe of *P. nilssoni* sp. nov. is gently and evenly curved (Fig. 6Ba), while that of *P. toxophorus* is more strongly and unevenly curved (Fig. 6Da). Parameres are gradually narrowing to their apex in *P. nilssoni* sp. nov., (Fig. 6Bbx) but they are distinctly tapered subapically in *P. toxophorus* (Fig. 6Dbx). Finally, the spermathecal spine in *P. nilssoni* sp. nov. (Fig. 8Ba) is curved unlike compared to other Indian species.

Etymology. The new species is dedicated to Dr. Anders N. Nilsson (Mullsjö, Sweden) for his immense contribution to aquatic Coleoptera. The name is a noun in the genitive case.

Collection circumstances. The species was collected in ponds with mud and rock as substratum. It was frequently found sympatrically with *P. quadricostatus* and sometimes with *P. toxophorus*.

Distribution. The distribution of the new species is confined so far to north-western, central and western India, namely Rajasthan, Madhya Pradesh and Maharashtra States. Some of the previous records of *P. toxophorus*, especially those from northern half of India, may actually also represent *P. nilssoni* sp. nov. and their revision is necessary.

3.3.3. *Peschetius quadricostatus* (Aubé, 1838)

Figs 5C, 6C, 8C

Hydroporus quadricostatus Aubé, 1838: 487 (original description; Bombay); Branden 1885: 61 (catalogue); Zimmermann 1920: 128 (catalogue); Régimbart 1899: 194 (description; new records).

Peschetius quadricostatus (Aubé): Guignot 1935: 131 (notes); 1942: 21 (new combination); Balfour-Browne 1946: 103 (taxonomic notes); Vazirani 1967: 108 (faunistics); Tonapi and Ozarkar 1969: 314, 315 (illustration, description, biology); Vazirani 1970a: 115 (description); 1970b: 445 (faunistics); 1972: 295 (faunistics, taxonomic notes); 1977a: 48 (catalogue); 1977b: 44 (faunistics); 1977c: 126 (faunistics); Brancucci 1979: 198 (faunistics and discussion); Vazirani 1981: 261 (faunistics); Nilsson 2001: 181 (catalogue); Biström and Nilsson 2003: 140 (description); Ghosh and Nilsson 2012: 32 (catalogue); Nilsson and Hájek 2021: 127 (catalogue); Jaiswal et al. 2020: 116 (diagnosis).

Specimens examined. Holotype: Not studied [not found in MNHN]. — **Other material:** INDIA – **Maharashtra** • 2 spec.; Jejuri; 18°16′39″N, 74°9′22″E; ca 750 m.a.s.l.; 1 Feb. 2014; S. D. Sheth leg.; reservoir; ZSIP • 1 spec; Sindhudurg, Madkhol; 15°56′49″N, 73°52′60″E; ca 50 m.a.s.l.; 27 May 2014; S. D. Sheth leg.; drying up river; ZSIP • 2 spec.; Raigad; 18°9′2″N, 73°24′8″E; ca 50 m.a.s.l.; 18 Feb. 2015; S. D. Sheth leg.; streamlet; HVGC • 2 spec.; Sindhudurg, Pendur; 16°4′9″N, 73°36′38″E; ca 10 m.a.s.l.; 4 May 2015; S. D. Sheth leg.; reservoir; UASB • 8 specs; Pune, Ane; 19°09′47″N 74°14′4″E; ca 800 m a.s.l.; 15 Sep. 2016; S. D. Sheth leg.; reservoir; HVGC • 2 spec., Igatpuri, 19°42.17′N, 73°33.06′E [19°42′11″N, 73°33′4″E]; 600 m.a.s.l.; 1 Aug.–12 Aug. 2002; P. Šípek and M. Fikáček leg.; NMPC • 2 spec.; Chiplun; [17°31′56″N, 73°30′55″E]; [ca 10 m.a.s.l.]; 10 Jun. 2006; V. Ryjáček leg.; NMPC • 32 spec.; Western Ghats Mts., Amboli env., 50 km W Belgaum, Daudki; [15°51′4″N, 74°29′52″E]; [ca 800 m.a.s.l.]; 21 May–23 May 2006; V. Ryjáček leg.; drying up river; NMPC. • 30 spec.; Western Ghats Mts., 10 km E Sawantwadi; [15°54′20″N, 73°49′17″E]; [ca 100 m.a.s.l.]; 22 May 2006; O. Šafránek leg.; JSCL, NMPC • 25 spec.; ca. 15 km E Savantvadi; 15°55′N 75°53′E [15°54′60″N, 73°52′60″E]; 40 m [ca 50 m.a.s.l.]; 22 May 2006; Z. Kejval leg.; riverside; NMPC. – **Madhya Pradesh** • 2 spec.; Panna NP; [24°43′8″N, 80°10′56″E]; [ca 400 m.a.s.l.]; 15 Aug. 1988; Werner leg.; HFCB • 1 spec.; ca. 130 km SE Bhopal, Pachmarhi env.; 22°28′N 78°26′E [22°27′60″N, 78°25′60″E]; ca. 1050 m.a.s.l.; 26 Jun.–29 Jun. 2006; Z. Kejval leg.; NMPC • 1 spec.; Hoshangabad Distr., ca. 5 km NE Hoshangabad, Bandrabhan, River Narmada; 22°47′29″N, 77°46′50″E, ca. 280 [300] m.a.s.l.; 23 Feb.–24 Feb. 2008; M. Jäch, S. and P. Sharma leg.; NHMW • 1 spec.; Chhindawara Distr., ca. 10 km E Matkuli, near Mahul Jhir E of Jhirpa, Bhadhua Chora (stream); 22°35′59″N, 78°35′30″E, 400 m.a.s.l.; 28 Feb. 2008; M. Jäch, S. and P. Sharma leg.; NHMW • 5 spec., Hoshangabad Distr., ca. 8 km SSE Matkuli, Satpura range, River Denwa, 22°34′29″N, 78°29′43″E; ca. 400 m.a.s.l.; 28 Feb. 2008; M. Jäch, S. and P. Sharma leg.; NHMW • 4 spec.; Hoshangabad Distr., Satpura Range, N part of Satpura NP, head of River Denwa Reservoir, Lagdha Beta, Sona Bhadra (stream); 22°31′38″N 78°11′18″E; 365 [ca 350] m.a.s.l.; 29 Feb. 2008; M. Jäch, S. and P. Sharma leg.; NHMW. – **Karnataka** • 2 spec.; Udupi Distr. E Bhatkal, Kollur; [13°51′48″N, 74°48′38″E]; [ca 100 m.a.s.l.]; 26 May–29 May 2006; Z. Kejval leg; NMPC. – Rajasthan • 2 spec.; Sariska; [27°15′55″N, 76°24′24″E]; [ca 400 m.a.s.l.]; 16 Aug. 1989; A. Riedel leg.; ZSMG • 1 spec.; NW Dungarpur, ca. 250 m along river;

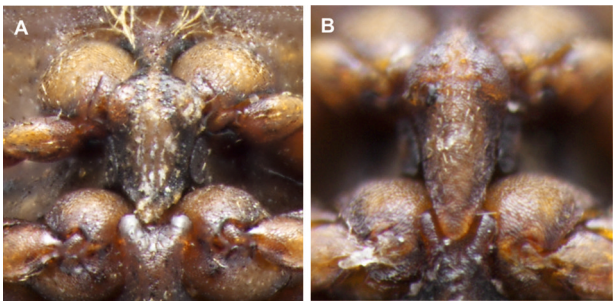

Figure 7. Prosternal process of *Peschetius*. **A** *P. bistroemi* sp. nov. (paratype; Mukkada, Kerala) **B** *P. nilssoni* sp. nov.(paratype; Jejuri, Maharashtra). Scale bars: without scale.

23°52′N 73°41′E [23°51′60″N, 73°40′60″E]; [ca 300 m.a.s.l.]; 1 Feb.–2 Feb. 2006; Z. Kejval leg; NMPC. – **Tamil Nadu** • 1 spec.; 5 km E Nagercoil; [8°11′9″N, 77°24′56″E]; [ca 50 m.a.s.l.]; 16 Jan. 1994; D. Boukal and Z. Kejval leg.; HFCB. – **Uttarakhand** • 1 spec.; Tanakpur; [29°03′60″N, 80°05′60″E]; [260 m.a.s.l.]; HGC; BMNH • 1 spec.; Haridvar, Chila; [29°56′46″N, 78°9′52″E]; 300 m.a.s.l.; 5 Aug.–14 Aug. 1994; M. Valenta leg.; ZSMG.

Redescription. Total length 3.10–3.45 mm and maximum width 1.65–1.85 mm (N = 25). See also Supplementary file 4. — Head ferruginous with two dark fronto-lateral spots (Fig. 5C). Pronotum ferruginous with bilobed black band along posterior margin and medial black streak along anterior margin. Elytron blackish with typical testaceous markings consisting of two subbasal spots, premedian and postmedian transverse bands and preapical spot. Punctation of head dense, distance between punctures smaller than puncture diameter. Punctures fine on clypeus, become progressively larger posteriorly on frons, occipital part posterior to eyes impunctate. Setiferous punctures present in shallow but distinct fronto-clypeal depressions and as a row along inner margin of eyes. Reticulation consisting of shallowly impressed, polygonal meshes on clypeus; posterior part of frons smooth. Impunctate occipital part posterior to eyes coarsely microreticulate. Pronotal disc with posterior depression less prominent but clearly distinguishable. Punctation dense, distances between punctures smaller than puncture diameter. Punctures setiferous, finer on disc, becoming coarser on margin and sides. Surface between punctures microreticulate with shallowly impressed, polygonal meshes. Elytra broadest at midlength, keels prominent. Punctation dense, distance between punctures approximately equal to puncture diameter. Punctures finer along suture, costae and lateral margin, coarser on disc. Surface between punctures microreticulate with well impressed polygonal meshes. Prosternal process elongate, narrowed at apex, apically keeled. Abdomen with five ventrites (V1 to V5); V1 with 6–9 macropunctures in one row while V2 with 3–5 macropunctures on each side, arranged randomly in two rows. Punctures on V2 to V5 setiferous; lateral depression on V3 to V5 prominent; reticulation of V2 to V5 consists of polygonal meshes. Median lobe of aedeagus gradually curved, tapering apically, apex pointed; with a basal process (Fig. 6Ca). Parameres with short setae in apical half, apex blunt, inner margin not sinuate (Fig. 6Cb). Spermatheca as in (Fig. 8C)—spermathecal spine straight, short and broad.

Collection circumstances. The species was found in pools, ponds, tanks, reservoirs and slow flowing streams, frequently with *P. nilssoni* sp. nov. This species was also found in the same habitat as *P. bistroemi* sp. nov in Aimcombu, Kerala.

Distribution. India (Bihar, Delhi, Goa, Gujarat, Jharkhand, Kerala, Madhya Pradesh, Maharashtra, Orissa, Tamil Nadu, Uttar Pradesh, West Bengal, Telangana), Nepal, Pakistan, Iran (Ghosh and Nilsson 2012; Jaiswal et al. 2020).

3.3.4. *Peschetius toxophorus* Guignot, 1942

Figs 5D, 6D, 8D

Peschetius toxophorus Guignot, 1942: 20 (original description; Mysore: Shimoga); Vazirani 1967: 108 (faunistics); 1970a: 113 (description); 1972: 295 (faunistics, taxonomic notes); 1977a: 48 (catalogue); 1977b: 44 (faunistics); 1977c: 126 (faunistics, taxonomic notes); Brancucci 1979: 198 (discussion); Vazirani 1981: 261 (faunistics); Nilsson 2001: 181 (catalogue); Biström and Nilsson 2003: 132 (description); Ghosh and Nilsson 2012: 33 (catalogue); Jaiswal et al. 2020: 114 (diagnosis); Nilsson and Hájek 2021: 127 (catalogue);
Peschetius andrewesi Balfour-Browne 1946: 104 (original description; India: Nilgiri Hills); synonymy by Guignot 1949: 16.

Specimens examined. Holotype: *P. toxophorus*: INDIA • ♀; Mysore [Karnataka], Shimoga [13°55′54″N, 75°34′4″E]; [ca 590 m.a.s.l.]; May 1936; MNHN. *P. andrewesi*: INDIA • ♂; Tamil Nadu; H.L. Andrewes leg.; BMNH • **Paratypes:** *P. andrewesi*: INDIA • 2 spec., Tamil Nadu, Nilgiri Hills; H.L. Andrewes leg.; BMNH• **Other material:** INDIA – **Maharashtra** • 3 spec.; Satara; 17°40′56″N, 73°58′16″E; ca 750 m.a.s.l.; 1 Sep. 2013; S. D. Sheth leg.; HVGC • 4 spec.; same collection data as for preceding; UASB • 1 spec.; Medha; 17°50′16″N, 73°49′22″E; ca 1250 m.a.s.l.; 30 Aug. 2013; S. D. Sheth leg.; ZSIP • 2 spec.; 40 km W Pune, Mulshi env., [18°30′5″N, 73°30′50″E]; [ca 650 m.a.s.l.]; 7 Oct.–11 Oct. 2005; J. Bezděk leg.; NMPC • 7 spec.; 4 km S Lonavala, Bushi [Bhushi] Dam env.; [18°42′8″N, 73°25′3″E]; 500 m.a.s.l.; 12 Oct.–15 Oct. 2005; J. Bezděk leg.; NMPC. – **Karnataka** • 2 spec., Chikkangalur; [13°19′1″N, 75°46′21″E] 1900 [ca 1050 m.a.s.l.]; Tabourel leg.; HFCB • 24 spec.; Chikmugalur; 12 Jun. 2004; ZSMG. – **Madhya Pradesh** • 1 spec., Hoshangabad Distr., Satpura Range, N part of Satpura NP, head of River Denwa Reservoir, Lagdha Beta, Sona Bhadra (stream); 22°31′38″N 78°11′18″E; 350 m.a.s.l.; 29 Feb. 2008; M. Jäch, S. and P. Sharma leg.; NHMW. – **Tamil Nadu** • 1 spec., Coimbatore; [11°1′1″N, 76°57′21″E]; 1400 ft [ca 450 m.a.s.l.]; Dec.1966; P.S. Nathan leg.; ZSMG • 3 spec., Nilgiri Hills, 15 km SE Kotagiri, Kunchappanai; 11°22′N 76°56′E [11°22′0″N, 76°55′60″E], 900 [ca 1000] m.a.s.l.; 13 May–20 May 1994; Z. Kejval leg.; NMPC • 124 spec.; same collection data as for preceding; 7 May–22 May 2000; D. Hauck leg.; JSCL, NMPC • 3 spec.; Vellore; [12°55′9″N, 79°7′56″E]; [ca 200 m.a.s.l.]; 10 Jun. 2004; Verner leg.; ZSMG.

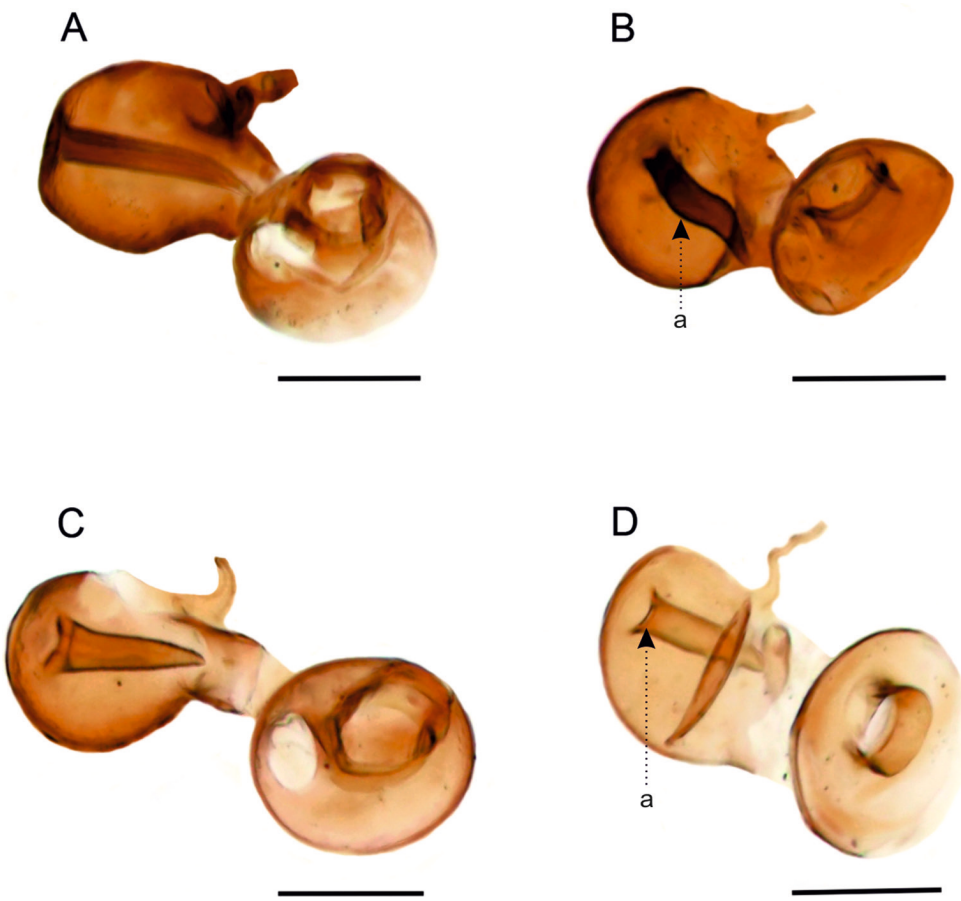

Figure 8. Female spermatheca of Indian *Peschetius*. **A** *P. bistroemi* sp. nov. (paratype; Mukkada, Kerala) **B** *P. nilssoni* sp. nov. (**a** spermathecal spine; paratype; Ane, Maharashtra) **C** *P. quadricostatus* (Ane, Maharashtra) **D** *P. toxophorus* (**a** spermathecal spine; Satara, Maharashtra). Scale bars: 100 µm (**A, B, C, D**).

Redescription. Total length 2.70–3.00 mm and maximum width 1.65–1.85 mm (N = 25). See also Supplementary file 4.

Head black except testaceous occipital part posterior to eyes (Fig. 5D). Pronotum testaceous with bilobed black band near posterior margin extending to posterior corners. Elytron blackish with typical testaceous markings consisting of two subbasal spots, premedian and postmedian transverse bands and preapical spot. Punctation of head dense, distance between punctures smaller than puncture diameter. Punctures fine on clypeus, become progressively larger posteriorly on frons, occipital part posterior to eyes impunctate. Setiferous punctures present in shallow but distinct fronto-clypeal depressions and as a row along inner margin of eyes. Reticulation consisting of polygonal meshes, impunctate occipital part coarsely microreticulate. Pronotal disc with posterior depression less prominent but distinguishable. Punctation dense, distances between punctures smaller than puncture diameter. Punctures setiferous, finer on disc, becoming coarser on margin and sides. Surface between punctures microreticulate with well impressed, polygonal meshes. Elytra broadest at midlength, keels prominent. Punctation dense, distance between punctures smaller than puncture diameter. Punctures finer along suture, costae and lateral margin, coarser on disc. Surface between punctures microreticulate, reticulation consisting of polygonal meshes. Prosternal process elongate, narrowed at apex, apically keeled, tuberculate in males. Abdomen with five ventrites (V1 to V5); V1 with 7–9 macropunctures arranged in one row while V2 with 4–7 macropunctures on each side, arranged in two rows randomly; punctation on V2 to V5 consisting of setiferous punctures; lateral depression on V3 to V5 prominent; reticulation of V2 to V5 consists of polygonal meshes. Ventral surface with large setiferous punctures. Median lobe strongly curved, tapering apically, apex pointed; with a basal process (Fig. 6Da). Parameres with long setae in apical 3/5th, apex rounded, inner margin strongly bisinuate (Fig. 6Db). Spermatheca as in (Fig. 8D)—spermathecal spine straight, short and broad.

Collection circumstances. The species was found inhabiting pools, ponds, tanks, reservoirs and slow flowing streams. In northern Maharashtra, the species was sometimes found sympatrically with *P. nilssoni* sp. nov.

Distribution. India; we have verified records from Karnataka, Maharashtra, Madhya Pradesh, Tamil Nadu and Telangana. The records from Andhra Pradesh, Bihar, Gujarat, Jharkhand, Kerala, Orissa and Rajasthan mentioned by Ghosh and Nilsson (2012) need to be revised with respect to *P. nilssoni* sp. nov.

3.3.5. Key to the species of *Peschetius* in India

1 Apex of prosternal process keeled; antennae in males not modified **2**
1' Apex of prosternal process not keeled; antennae in males modified, fourth and fifth antennomeres distinctly swollen, sixth and seventh ventrally flat (Fig. 5A)..... ***P. bistroemi* sp. nov.**
2 Head pale with small fronto-lateral spots near eyes (Fig. 5C); median lobe gradually curved (Fig. 6Ca), parameres broad at apex and with sparse setae (Fig. 6Cb)..... ***P. quadricostatus* (Aubé, 1838)**
2' Head dark except for occipital region (Fig. 5B, D) **3**
3 Transverse elytral premedian testaceous band separated into two spots; elytra widest before midlength; median lobe of male genitalia evenly curved (Fig. 6Ba); spermathecal spine sinuous (Fig. 8B) ..... ***P. nilssoni* sp. nov.**
3' Transverse elytral premedian testaceous band continuous; elytra widest at midlength; median lobe of male genitalia not evenly curved (Fig. 6Da); spermathecal spine straight (Fig. 8D)..... ***P. toxophorus* Guignot, 1942**

4. Discussion

Peschetius bistroemi sp. nov. from Kerala is rather unique as it is the only known member of the genus with broadened male antennomeres; its weakly supported distant placement compared to other Indian species is most likely due to insufficient sampling. The diagnostically distinct prosternal processes of *P. bistroemi* sp. nov. and Sri Lankan endemic *P. taprobanicus* are similar, indicating a possible close relationship between these two species. However, *P. bistroemi* sp. nov. differs from the latter in the shape of its male genitalia. Therefore, more work including a better sampling of African and the Sri Lankan species, and multigene phylogeny is definitely necessary to clarify the position of *P. bistroemi* sp. nov. Moreover, based on the preliminary data, *P. bistroemi* sp. nov. is described from the region between geologically ancient Palghat and Shencottah gaps in the Western Ghats (Fig. 1). Various studies have reported the role of these gaps as biogeographical barriers leading to genetic variation and speciation in the case of flora, and fauna including both vertebrates and invertebrates (e.g. Vidya et al. 2005; Bahulikar et al. 2006; Joshi and Karanth 2013; Anoop et al. 2018). Additionally, many endemic and threatened freshwater fishes of Kerala, for example *Travancoria elongata* Pethiyagoda & Kottelat, 1994 are known to inhabit the River Chalakudy (Raghavan et al. 2008) that originates south of the Palghat Gap (Arunachalam 2000). Therefore, extensive sampling of water beetles over a wide geographical range together with the afore-mentioned barriers is needed to understand biogeography of *P. bistroemi* sp. nov.

On the other hand, the second newly described species, *Peschetius nilssoni* sp. nov. is without any doubt closely related to *P. toxophorus*. Interestingly, at the beginning of the 20th Century, French specialist Maurice Régimbart correctly recognised two *Peschetius* morphospecies with dark head within the material in BMNH and labelled them as two new species. However, he did not describe them, and Balfour-Browne (1946) mixed both taxa under his *P. andrewesi*. Subsequently, Vazirani (1977c) mentioned the differences in elytral pattern of 'two forms of *P. toxophorus*' and predicted the presence of another undescribed *Peschetius* species in the Western Ghats. Yet, the species remained unrecognised for another 40 years, until the present integrative approach of morphological study, morphometry and molecular analysis confirmed its status and enabled us to describe the new species. Despite being found sympatrically, we did not encounter any specimen showing intermediate characters between *P. quadricostatus* or *P. toxophorus* and this new species. Further, molecular analysis has shown that the inter-specific genetic distance between *P. nilssoni* sp. nov. and its sister taxa *P. toxophorus,* is comparatively smaller (2.7–3.3%) than inter-specific genetic distances between the other *Peschetius* species studied here, and for the other species for which molecular data are available. Both the genetic methods of species delimitation, ASAP and GMYC, clearly identified *P. nilssoni* sp. nov. and *P. toxophorus* as distinct, reciprocally monophyletic species.

Low genetic distances among species have been previously reported for several insect taxa, for example, 2.2% inter-species divergence has been observed in certain Australian insects (Pons et al. 2006). The known genetic distance within Coleoptera using *cox1* ranges from 2.0 to 4.0% (Hendrich et al. 2010; Ribera et al. 2010; Abellán et al. 2012). Similarly, in the predaceous diving beetle genus *Antiporus*, the known genetic divergence between species ranges from 3.5 to 6.6% (Hawlitschek et al. 2011). A low genetic divergence may suggest relatively recent speciation event between the two species.

Our integrative taxonomic approach towards understanding the diversity of aquatic beetles not only unveiled two new species of *Peschetius* but also provided interesting insights, albeit preliminary, into the ecology and evolution of these species. Our study suggests that such an approach can provide better understanding of diversity of invertebrate taxa in the Western Ghats. Both the species of *Peschetius* described in this work belong to the Western Ghats-Sri Lanka biodiversity hotspot (Myers et al. 2000), reemphasizing its importance as high biodiversity reserve also with respect to its invertebrate fauna. While insects play a vital role in ecosystem functioning, these have often been neglected compared to vertebrate taxa (Goulson 2019). Diversity of the invertebrate fauna in the Western Ghats is riddled with Linnean shortfall (Brown and Lomolino 1998) owing to limited taxonomic studies in this region. Despite the presence of unique habitats in

the Western Ghats the studies on its invertebrate fauna are limited (Myers et al. 2000). Further, Short (2018) emphasized the need of thorough inventory work on water beetles with the possibility of discovery of novel species from southeast Asia including India. Given that Linnean shortfall compromises biodiversity knowledge essential for evolutionary, ecological and conservation research (Hortal et al. 2015) overcoming the shortfall is essential (Bini et al. 2006). Freshwater ecosystems are among the most threatened habitats in the anthropocene and dedicated efforts to their conservation are essential (Dudgeon 2019).

5. Conclusion

The combined approach of morphology, geometric morphometry and molecular analysis revealed the presence of four *Peschetius* species in India; two species from Western Ghats biodiversity hotspot are described as new to science. While one of those species was collected only recently, the second was known but remained unrecognised for more than 100 years. Therefore, the integrative taxonomic approach is considered important for the study of the biodiversity.

6. Authors' contributions

SDS performed fieldwork, museum study, morphological and molecular work, and data analysis. JH, HVG and SDS studied and identified material. SDS and JH contributed to preparation of illustrations. ND verified and analyzed data; helped planning a part of the fieldwork; supervised both laboratory work and data analysis of SDS. HVG provided inputs for data analyses. JH corrected, revised and discussed the data.

All authors collaborated in the development of the research problem identified by HVG, discussed results and contributed for the manuscript preparation.

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8. Competing interests

The authors have declared that no competing interests exist.

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Appendix 1

Appendix. Habitats of new species of *Peschetius*. **A** roadside streamlet in Pambady (Kerala), type locality of *P. bistroemi* sp. nov. **B** streamlet in Aimcombu (Kerala; *P. bistroemi* sp. nov.) **C** roadside reservoir in Ane (Maharashtra), type locality of *P. nilssoni* sp. nov. **D** roadside pond in Satara (Maharashtra; *P. nilssoni* sp. nov.)

Supplementary material 1

Table S1

Authors: Sheth SD, Ghate HV, Dahanukar N, Hájek J (2021)
Data type: .xlsx
Explanation note: List of specimens studied in the DarwinCore format.
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Link: https://doi.org/10.3897/asp.79.e68203.suppl1

Supplementary material 2

Figure S1

Authors: Sheth SD, Ghate HV, Dahanukar N, Hájek J (2021)
Data type: .xlsx
Explanation note: Results of genetic species delimitation using assemble species by automatic partitioning (ASAP) analysis. **A** Statistics of species delimitation. Row highlighted in red is the best partition with the lowest ASAP score and identifies six species which include four species of *Indian Peschetius* (*P. bistroemi* sp. nov., *P. nilssoni* sp. nov., *P. quadricostatus* and *P. toxophorus*), one species of African Peschetius (*P. nodieri*) and the outgroup (*Amarodytes* sp.). **B** ASAP score versus the p distances. **C** Neighbor joining tree with species delimitation (green line) based on best partition identified by ASAP score.
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Link: https://doi.org/10.3897/asp.79.e68203.suppl2

Supplementary material 3

Figure S2

Authors: Sheth SD, Ghate HV, Dahanukar N, Hájek J (2021)
Data type: .xlsx
Explanation note: Results of genetic species delimitation using General mixed Yule-Coalescent (GMYC) analysis. **A** Number of maximum likelihood (ML) entities versus relative time of divergence. **B** Likelihood versus relative time. **C** Bayesian ultrametric tree with maximum likelihood entities demarcated by red line. GMYC analysis identifies six ML entities which include four species of Indian Peschetius (*P. bistroemi* sp. nov., *P. nilssoni* sp. nov., *P. quadricostatus* and *P. toxophorus*), one species of African Peschetius (*P. nodieri*) and the outgroup (*Amarodytes* sp.).
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Link: https://doi.org/10.3897/asp.79.e68203.suppl3

Supplementary material 4

Table S2

Authors: Sheth SD, Ghate HV, Dahanukar N, Hájek J (2021)
Data type: .xlsx
Explanation note: Morphometry data of Indian Peschetius, all values in mm.
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Link: https://doi.org/10.3897/asp.79.e68203.suppl4