

# Review of the genus *Endothyrella* Zilch, 1960 with description of five new species (Gastropoda, Pulmonata, Plectopylidae)

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## Abstract

All known taxa of the genus *Endothyrella* Zilch, 1960 (family Plectopylidae) are reviewed. Altogether 23 *Endothyrella* species are recognized. All species are illustrated and whenever possible, photographs of the available type specimens are provided. Five new species are described: *E. angulata* Budha & Páll-Gergely, **sp. n.**, *E. dolakhaensis* Budha & Páll-Gergely, **sp. n.** and *E. nepalica* Budha & Páll-Gergely, **sp. n.** from Nepal, *E. robustistriata* Páll-Gergely, **sp. n.** from the Naga Hills, India, and *E. inexpectata* Páll-Gergely, **sp. n.** from Sichuan, China. *Helix* (*Plectopylis*) *municipurensis* Godwin-Austen, 1875 is synonymized with *Helix* (*Plectopylis*) *serica* Godwin-Austen, 1875, and *Plectopylis* (*Endothyra*) *gregorsoni* Gude, 1915 is synonymized with *Helix* (*Plectopylis*) *macromphalus* W. Blanford, 1870. *Plectopylis plectostoma* var. *exerta* Gude, 1901 is a synonym of *Plectopylis plectostoma* var. *tricarinata* Gude, 1896, which is a species in its own right. Five species of the genus *Chersaecia* viz. *Plectopylis* (*Chersaecia*) *bedfordi* Gude, 1915, *Helix* (*Plectopylis*) *brahma* Godwin-Austen, 1879, *Helix* (*Plectopylis*) *Oglei* Godwin-Austen, 1879, *Helix* (*Plectopylis*) *serica* Godwin-Austen, 1875, and *Plectopylis* (*Endothyra*) *williamsoni* Gude, 1915 are moved to *Endothyrella*. The holotype of *Plectopylis hanleyi* Godwin-Austen, 1879 seems to be lost; therefore, *P. hanleyi* is considered to be a *nomen dubium*.

## Keywords

Taxonomy, anatomy, India, Nepal, China, Myanmar, sinistrality

## Introduction

The Plectopylidae Möllendorff, 1898 are a land snail family of the superfamily Plectopyloidea that ranges across large parts of southeast Asia from Nepal to southern Japan (Gude 1899d, Páll-Gergely and Hunyadi 2013). Schileyko (1999) classified two families in the Plectopyloidea: the Plectopylidae and the mainly Sri Lankan Corillidae Pilsbry, 1905. Other authors (Zilch 1960, Bouchet and Rocroi 2005) also included the African Sculptariidae Degner, 1923 in the superfamily. Historically, the family name Corillidae (e.g. Yen 1939 and Zilch 1960) or the heliced subfamily Corillinae (in Gude 1914b) have been applied to the current concept of Plectopyloidea. The Chinese *Amphicoelina* Haas, 1933 has been included in the Corillidae or the Plectopylidae by Yen (1939), Zilch (1960) and Schileyko (1999). That genus, however, likely belongs to the Camaenidae (see Páll-Gergely and Asami 2014), as originally proposed by Haas (1933). The Plectopylidae differ from the Corillidae by the presence of one or two vertical (= perpendicular to the suture) lamellae on the parietal wall, approximately a quarter to a half whorl behind the aperture. In contrast, the Corillidae have only horizontal (= parallel with the suture) parietal plicae (in *Corilla* all plicae may be absent).

Gude revised every known taxon of *Plectopylis* Benson, 1860 at the end of the 19<sup>th</sup> century, and published drawings of their shells and armature (lamella complex) (see citations in Richardson 1986). He subdivided *Plectopylis* into seven “sections” (Gude 1899c): *Endothyra* Gude, 1899c, *Chersaecia* Gude, 1899c, *Endoplion* Gude, 1899c, *Plectopylis*, *Sinicola* Gude, 1899c, *Enteroplax* Gude, 1899d and *Sykesia* Gude, 1897f. *Enteroplax* was transferred to the Strobilopsidae Wenz, 1915 (Solem 1968, Schileyko 1998), and *Ruthvenia* Gude, 1911 (replacement name for *Sykesia* which itself was a replacement name for *Austenia* Gude, 1897e) to the Endodontidae Pilsbry, 1895 (Gude 1914b, Schileyko 2001) or to the Charopidae Hutton, 1884 (Schileyko 2010, Raheem et al. 2014). The name *Endothyrella* was established by Zilch (1960) to replace *Endothyra* Gude, 1899, a junior homonym of *Endothyra* Phillips, 1845 (Foraminifera).

Gude’s (1899c) diagnoses of his sections are based on the direction of the coiling of the shell, the depth of the umbilicus, and the morphology and direction of the palatal folds. Most of his diagnoses are not mutually exclusive. Recent revisions of the genera *Endoplion* and *Sinicola* (Páll-Gergely and Hunyadi 2013, Páll-Gergely and Asami 2014, and Páll-Gergely et al. 2015) showed that the species assigned to these two genera should be classified within multiple genera and the genera should be re-diagnosed. Moreover, several species were misassigned by Gude (1899c), which was probably the result of focusing exclusively on the morphology of the parietal plicae.

The aim of this paper is to review and diagnose all *Endothyrella* species, publish images of the type specimens where possible, provide a diagnosis of *Endothyrella*, and

delimit it from other plectopylid genera. Ongoing revision of the genera *Chersaecia* and *Plectopylis* revealed that *Chersaecia* sensu Gude (1899c, 1915) worked as a “garbage can” including species that could not be classified within other sections. Revising the validity of *Chersaecia* species is beyond the scope of the present paper. However, three sinistral (*bedfordi*, *brahma*, *williamsoni*) and two dextral (*oglei*, *serica*) species are moved from *Chersaecia* to *Endothyrella*, mainly based on the sculpture of the embryonic whorls and the absence of the apertural fold. Additionally, five new *Endothyrella* species are described from Nepal, India, and China.

### Taxonomic history of *Endothyrella* and *Chersaecia* species

*Endothyrella plectostoma* was the first described species that is currently placed in the Plectopylidae. It was introduced as *Helix plectostoma* by Benson (1836), who classified it within the subgenus *Helicodonta* and who mentioned that because of its angulated periphery it shows connection towards the subgenus *Helicigona*. In modern classifications *Helicodonta* and *Helicigona* belong to the families Helicodontidae and Helicidae, respectively, and both are the members of the superfamily Helicoidea (Schileyko 2006a, 2006b). Benson (1836) compared *Helix plectostoma* with *H. personata*, (= *Isognomostoma isognomostomos* [Schröter, 1784], family Helicidae) and *H. corcyrensis* (= *Lindholmiola corcyrensis* [Rossmässler, 1838], family Helicodontidae).

The helicid subgenus *Plectopylis* was erected by Benson (1860) for six species subdivided into three unnamed “sections”. His third section is equivalent with Gude’s (1899c) *Endothyra*, and contained *H. plectostoma* and *H. pinacis* Benson, 1859. Gude (1899c) diagnosed *Endothyra* as follows: “Sinistral. Umbilicus moderate. Palatal folds horizontal or oblique”. He selected *Helix plectostoma* as the type species and classified the following species in *Endothyra*: *minor* Godwin-Austen, 1879b, *hanleyi* Godwin-Austen, 1879b, *blanda* Gude, 1898, *macromphalus* W. Blanford, 1870, *sowerbyi* Gude, 1898, *plectostoma* Benson, 1836 (including *prodigium* Benson and *tricarinata* Gude, 1896), *affinis* Gude, 1897b, *pinacis* (including *pettos* von Martens, 1868), and *fultoni* Godwin-Austen, 1892.

Simultaneously, Gude (1899c) diagnosed the “section” *Chersaecia* as follows: “Sinistral or dextral. Umbilicus wide. Palatal folds horizontal or oblique. Sometimes with one oblique or vertical plate”. He selected *Plectopylis leiophis* Benson, 1860 as type species and classified the following species in *Chersaecia*: *muspratti* Gude, 1897, *austeni* Gude, 1899b, *oglei* Godwin-Austen, 1879a, *serica* Godwin-Austen, 1875, *municipurensis* Godwin-Austen, 1875, *nagaensis* Godwin-Austen, 1875, *pseudophis* “Blanford” in Godwin-Austen, 1875, *leiophis*, *refuga* Gould, 1846, *perrieriae* Gude, 1897, *shiroiensis* Godwin-Austen, 1875, *perarcta* W. Blanford, 1865, *brachydiscus* Godwin-Austen, 1879a, *dextrorsa* Benson, 1860, *shanensis* Stoliczka, 1873, *brahma* Godwin-Austen, 1879a, *andersoni* W. Blanford, 1869, and *laomontana* Pfeiffer, 1863. An additional *Chersaecia* species (*Plectopylis kengtungensis* Gude, 1914a) was described later.

From the shells collected during the Abor Expedition (Abor Country, north-eastern India), Gude (1915) described seven *Plectopylis* species, classifying them in the subgenera *Endothyra* (*oakesi*, *gregorsoni*, *miriensis*), *Chersaecia* (*williamsoni* and *bedfordi*), *Endoplon* (*aborensis*) and *Sinicola* (*babbagei*). Gude (1915) apparently relied only on the morphology of the palatal plicae. In case of *williamsoni* and *bedfordi*, Gude (1915) mentioned that they are closely related to *Plectopylis* (*Chersaecia*) *brahma*. The subgeneric classification of *P. aborensis* is based on its palatal plicae, which resemble those of *Plectopylis* (*Endoplon*) *brachyplecta*, whereas those of *Plectopylis babbagei* resemble those of *Plectopylis pulvinaris*, a species classified within the subgenus *Sinicola* by Gude (1899c). After Gude (1915), only two new species were added to *Chersaecia*, viz. *Plectopylis* (*Chersaecia*) *degerbolae* Solem, 1966 and *P. (Ch.) simplex* Solem, 1966. *Plectopylis babbagei* and *P. aborensis* were moved to *Endothyrella* by Páll-Gergely and Hunyadi (2013).

## Material and methods

Shell whorls were counted according to Kerney and Cameron (1979: 13) (precision 0.25 mm). Differences in size are indicated in the diagnosis using the following terms: tiny (smaller than 6 mm), very small (6–10 mm), small (10–15 mm), medium-sized (15–20 mm), large (20–25 mm), very large (25–30 mm).

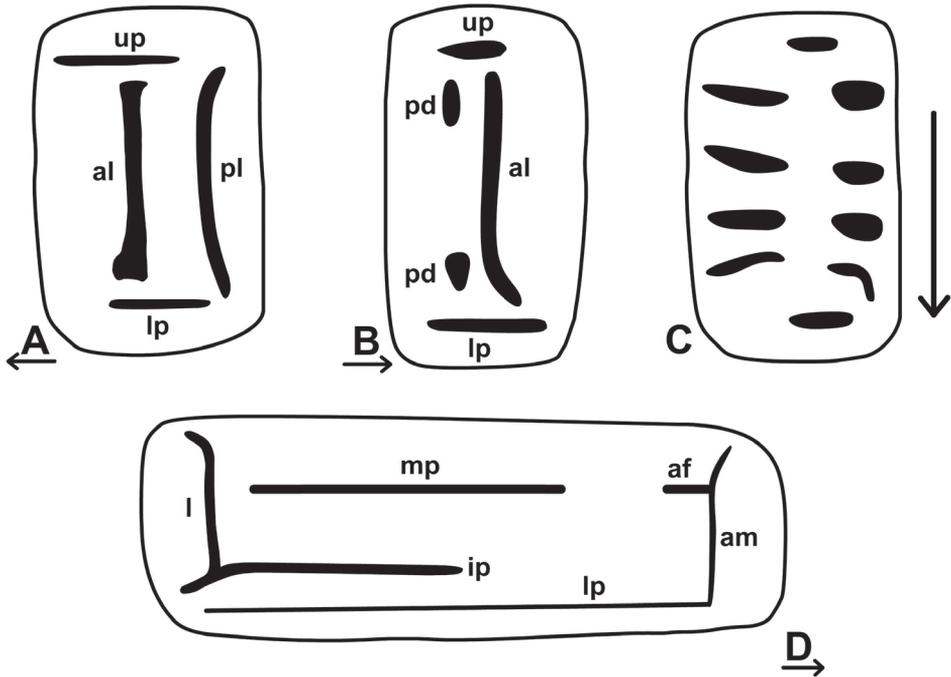
For the nomenclature of lamellae (vertical parietal folds) and plicae (horizontal parietal folds and palatal folds) see Figure 1. Whenever possible, the internal lamellae and plicae have been exposed by removing the shell wall at the appropriate part of the shells (inner view). Yet, if damaging the shells was not an option (because too few shells available), the plicae were figured on the basis of their visibility through the shell wall (outer view). “Anterior” refers to the part or side of the armature in direction of the aperture, “posterior” refers to the other side of the armature.

For each taxon, the specimens studied are listed separately as types, museum material and new material. Geographic names mentioned in the literature and on labels (Table 1) were searched using Google, Google Earth and Lozupone et al. (2004). Locality names are copies from the labels and from the literature with original spelling. Therefore the same locality might present with more than one spelling (e.g. Sikkim/Sikhim, Sadia/Sadiya, Khasi/Khasia).

Ethanol-preserved specimens were dissected under a Leica stereomicroscope, equipped with a photographic camera. In description of the reproductive system, we used the terms “proximal” and “distal” relative to the centre of the body.

Individual buccal masses was removed and soaked in 2 M KOH solution for 5 h before extracting the radula, which was preserved in 70% ethanol. Radulae and shells were directly observed without coating under a low vacuum SEM (Miniscope TM-1000, Hitachi High-Technologies, Tokyo).

The dates of publication of the Proceedings of the Zoological Society of London follows Duncan (1937).



**Figure 1.** Nomenclature of parietal (**A, B, D**) and palatal (**C**) plicae and lamellae. **A** shows a “*Gudeodiscus*-type” plication with two lamellae **B** shows a usual *Endothyrella* lamellation **D** shows a “*Chersaecia*-type” lamellation with long lower plica and middle plica not connected to the apertural fold (in most species however, they are connected forming a continuous plica). Small arrows under the letters show the direction of the aperture (**A** shows dextral, **B** and **D** sinistral specimen). Large arrow next to **C** shows the direction of counting of palatal plicae (first above, last below). Abbreviations: af: apertural fold; al: anterior lamella; am: apertural margin (peristome); ip: intermediate plica; l: lamella; lp: lower plica; mp: main plica; pl: posterior lamella; pd: posterior denticles; pl: posterior lamella; up: upper plica. Note that there are upper and lower plicae on both (palatal and parietal) walls.

### Taxonomic treatment

All available type material of each *Chersaecia* taxon deposited in the MCZ, NHMUK, SMF and ZMUC have been examined. The type specimens of *Endothyrella* taxa examined are mentioned under each species.

The following shell characters of species formerly classified in *Chersaecia* and *Endothyrella* were examined in order to revise the generic assignment and diagnose genera: (1) coiling direction; (2) sculpture of the protoconch; (3) presence or absence of the apertural fold; morphology of the parietal plicae and lamellae, namely (4) the presence/absence/length of a horizontal main plica, (5) the presence/absence/length of a lower plica, and (6) the presence or absence of additional denticles behind the lamella; (7) morphology of middle palatal plicae (the first and last are straight in almost all cases); and the (8) presence/absence/morphology of hairs.

**Table 1.** Geographic names mentioned in the literature and on labels of *Endothyrella* Zilch, 1960 taxa. Asterisks indicate names with unknown exact localities.

Locality	Region	Taxon
Abor Hills	India, Arunachal Pradesh	<i>williamsoni</i>
Arakan Hills (= Rakhine)	Myanmar, Rakhine district	<i>plectostoma</i>
Bassein (= Pathein)	Myanmar, Ayeyarwady district: 16°47'N, 94°44'E	<i>plectostoma</i>
Brahmakund	India, Assam: 27°51.4'N, 96°22'E	<i>brahma</i>
Burrail (= Barail) Gorge	India, mountain range centered 70 km NE Silchar (Assam)	<i>macromphalus</i> , <i>plectostoma</i>
Cachar (= Katchar)	India, District in Assam: 24°46'N, 92°50'E	<i>affinis</i> , <i>blanda</i> , <i>plectostoma</i> , <i>serica</i>
Cherra Poonjee (= Cherrapunji)	India, Meghalaya, Khasi Hills: 25°18'N, 91°42'E	<i>affinis</i> , <i>fultoni</i> , <i>plectostoma</i> , <i>tricarinata</i>
Chittagong	City in Bangladesh: 22°22'N 91°48'E; also name of a district	<i>plectostoma</i>
Damsang Peak	India, Sikkim	<i>blanda</i> , <i>pinacis</i>
Darjiling (= Darjeeling)	India, town in West Bengal: 27°2'N, 88°15.5'E	<i>blanda</i> , <i>macromphalus</i> , <i>minor</i> , <i>pinacis</i> , <i>plectostoma</i>
Dihang (= Siang) River	India, Arunachal Pradesh: river flows to the Brahmaputra at 27°50'N, 95°27'E	<i>bedfordi</i> , <i>oakesi</i>
Dunsiri (= Dhansiri) River	India, river flows to the Brahmaputra at 26°42'N, 93°35'E	<i>plectostoma</i>
Durrang (= Darrang)	India, district in Assam: centered at 26°26'N, 92°1.5'E	<i>plectostoma</i>
Garo Hills	India, Western Meghalaya: 25°28'N, 90°20'E	<i>plectostoma</i>
Ghoramara	Bangladesh, town approx. 15 km NW from Chittagong, at 22°29'N 91°43'E	<i>plectostoma</i>
Prov. Harenni*	Myanmar	<i>plectostoma</i>
Hengdan*	India, mountain in northern Cachar Hills	<i>serica</i>
Ihang River*	India, Manipur	<i>robustistriata</i> sp. n., <i>serica</i>
Japvo Peak	India, highest mountain in Naga Hills: 25°36'N, 94°4'E	<i>serica</i>
Karenni (= Kayah) State	state located south of Shan State, Myanmar	<i>plectostoma</i>
Khasi (= Khasia) Hills	India, Meghalaya	<i>affinis</i> , <i>fultoni</i> , <i>macromphalus</i> , <i>minor</i> , <i>pinacis</i> (?), <i>plectostoma</i> , <i>sowerbyi</i> , <i>tricarinata</i>
Khunho (= Khono) Mountain	India, Naga Hills: 25°31.3'N, 94°6.5'E	<i>serica</i>
Kohima	India, town in SE Nagaland: 25°40'N, 94°6.5'E	<i>serica</i>
Kopamedza ridge*	India, Daffa Hills, Barail Range	<i>serica</i>
Laisen Peak*	India, Manipur	<i>robustistriata</i> sp. n.
Lhota Naga*	India, Nagaland, Naga Hills	<i>robustistriata</i> sp. n.
Lopchu	India, Sikkim 27°7.5'N, 88°25'E	<i>pinacis</i>
Luyor Peak	India, Abor county, Arunachal Pradesh: 28°45'N, 95°45'E	<i>babbagei</i>
Mairung (= Mairang)	India, village in Meghalaya, Khasi Hills: 25°34.2'N, 91°37.8'E	<i>macromphalus</i>
Miri Hills	India, on the border between Assam and Arunachal Pradesh	<i>miriensis</i>
Munipur (= Manipur)	India, Manipur	<i>plectostoma</i> , <i>robustistriata</i> sp. n., <i>serica</i>
Naga Hills	on the border of Nagaland (India) and Myanmar	<i>blanda</i> , <i>macromphalus</i> (?), <i>minor</i> (?), <i>plectostoma</i> , <i>plectostoma</i> , <i>serica</i>

Locality	Region	Taxon
Naraindher*	India, Assam, Cachar district	<i>affinis</i>
Pankabari (= Pankhabari)	India, northern part of West Bengal: 26°50'N, 88°16'E	<i>pinacis</i>
Pegu (= Bago)	Myanmar, Bago District: 17°20'N, 96°29'E	<i>plectostoma</i>
Picholanulla*	India, probably Daffa Hills	<i>plectostoma</i>
Pyema Khyoung	Myanmar, Ayeyarwady district	<i>plectostoma</i>
Rarhichu (= Rungpo?)*	India, Sikkim	<i>blanda, minor, pinacis</i>
Renging (= Rengging)	India, Abor county, Arunachal Pradesh: 28°9'N, 95°15.5'E	<i>aborensis</i>
Richila (Rechila) Peak	India, Sikkim: 27°8'N, 88°45'E	<i>blanda</i>
Rinkpo valley*	India, Sikkim	<i>blanda</i>
Rissetchu*	India, Sikkim	<i>blanda</i>
Riu*	India, Abor Hills	<i>oakesi</i>
Rotung (= Rottung)	India, Abor county, Arunachal Pradesh: 28°8'N, 95°8.5'E	<i>aborensis</i>
Rungmaval*	India, Sikkim	<i>pinacis</i>
Rungun*	India, probably Sikkim	<i>minor, pinacis</i>
Sadia (Sadiya)	India, Assam: 27°51.6'N, 95°37.6'E	<i>oglei</i>
Salwen (= Salween) River	River in China and eastern Myanmar	<i>plectostoma</i>
Shillong	India, city in Meghalaya, Khasi Hills	<i>macromphalus</i>
Shiroifurar peak (probably Shirui Hills)	India, NE Manipur: 25°6.3'N 94°27.4'E	<i>plectostoma</i>
Shweego (probably Shwegu)	probably Myanmar, Kachin District: 24°12'N, 96°48'E	<i>plectostoma</i>
Sibbum (= Sibum)	India, Abor Hills: 28°19'N, 95°9'E	<i>oakesi</i>
Sigon (= Siyom) River	India, river runs into the Siang River at 28°14'N, 95°E	<i>bedfordi</i>
Singging*	India, Abor Hills	<i>oakesi</i>
Sylhet	Bangladesh, Sylhet Division, Sylhet city: 24°54'N, 91°52'E	<i>plectostoma, serica</i>
Teria Ghat	India, Khasi Hills	<i>macromphalus, plectostoma</i>
Tongoop*	Myanmar, Rakhine district	<i>plectostoma</i>
Torúpútú*	India, Daffa Hills	<i>robustistriata</i> sp. n.
Tsanspu (= Tsangpo) River	India (Tibetan name of the Brahmaputra River)	<i>bedfordi</i>
Yamne River	India, Abor Hills, river flows into the Siang River at 28°10.5'N, 95°13'E	<i>gregorsoni, oakesi</i>
Ywathit (= Ywarthit)	Village (?) in Kayah State, Myanmar: 19°10'N 97°30'E	<i>plectostoma</i>

This taxonomic revision of *Endothyrella* species is based on morphology by examination of specimens and literature. The present species are defined based on unique combinations of morphological traits, some of which are discrete in nature (e.g. presence or absence of periostracal filaments) or continuous but with distinct gaps (e.g. height of the spire). No specimens were found that show transitional characters between probably sympatric morphospecies (Table 2). Although we have no, or too little, information on the genetic, physiological and/or ecological basis of the phenotypic characters used to describe the species in this work, we putatively interpret the diagnostic phenotypic differences under the biological species concept (Mayr 1942), i.e. as markers of reproductive isolation. However, the biological species concept is not

**Table 2.** Co-occurrence of *Endothyrella* Zilch, 1960 species. Two stars indicate that the two species were collected at geographically close sites (*nepalica-minor*: 2680 m). One star indicates presence of the two species mixed within museum samples.

	<i>nepalica</i> sp. n.	<i>blanda</i>	<i>macromphalus</i>	<i>tricarinata</i>	<i>sowerbyi</i>	<i>affinis</i>
<i>affinis</i>		*	*			
<i>minor</i>	**	*	*			
<i>pinacis</i>		*				
<i>blanda</i>			*		*	
<i>plectostoma</i>		*		*	*	*

applicable to specific identification of allopatric populations regardless of their morphological differences. The shell shape, the characters of the armature and the shell sculpture was of primary important in recognizing allopatric species. In some cases we found stable but minor differences of allopatric populations, such as the divided/not palatal plicae in *Plectopylis macromphalus* and not divided ones in *Plectopylis gregorsoni* and the difference in the spaces between hair rows in Nepalese versus Indian populations of *E. minor*. In those cases we handled these forms under a single specific name. No subspecific differentiation is applied because most samples are provided with poor locality data which, in most cases, does not provide a clear understanding on the distribution of certain morphological forms.

## Abbreviations

<b>CDZMTU</b>	Central Department Zoology Museum of Tribhuvan University (Kathmandu, Nepal)
<b>D</b>	shell diameter
<b>H</b>	shell height
<b>HA</b>	Collection András Hunyadi (Budapest, Hungary)
<b>HNHM</b>	Hungarian Natural History Museum (Budapest, Hungary)
<b>JUO</b>	Collection Jamen Uiriamu Otani (Osaka, Japan)
<b>MCZ</b>	Museum of Comparative Zoology (Massachusetts, USA)
<b>MMGY</b>	Mátra Múzeum, Gyöngyös, Hungary
<b>NHM</b>	The Natural History Museum (London, UK)
<b>NHMSB</b>	Natural History Museum, Sibiu (Romania), Bielz collection
<b>NHMUK</b>	When citing NHM registered specimens
<b>NHMW</b>	Naturhistorisches Museum Wien (Vienna, Austria)
<b>NMBE</b>	Natural History Museum, Bern, Switzerland
<b>SMF</b>	Senckenberg Forschungsinstitut und Naturmuseum (Frankfurt am Main, Germany)

<b>TH</b>	Collection Takashi Hosoda (Kofu, Japan)
<b>UMZC</b>	University Museum of Zoology (Cambridge, UK)
<b>Wh</b>	number of whorls
<b>WM</b>	Collection Wim J. M. Maassen (Echt, The Netherlands)
<b>ZMB/MOLL</b>	Museum für Naturkunde (Berlin, Germany)
<b>ZMH</b>	University of Hamburg (Hamburg, Germany)
<b>ZMUC</b>	Zoological Museum, University of Copenhagen (Denmark)
<b>ZSI</b>	Zoological Survey of India

## Systematic Part

### Family Plectopylidae Möllendorff, 1898

#### Genus *Chersaecia* Gude, 1899

1899c *Chersaecia* (section of the genus *Plectopylis*) Gude: Science Gossip, 6: 148.

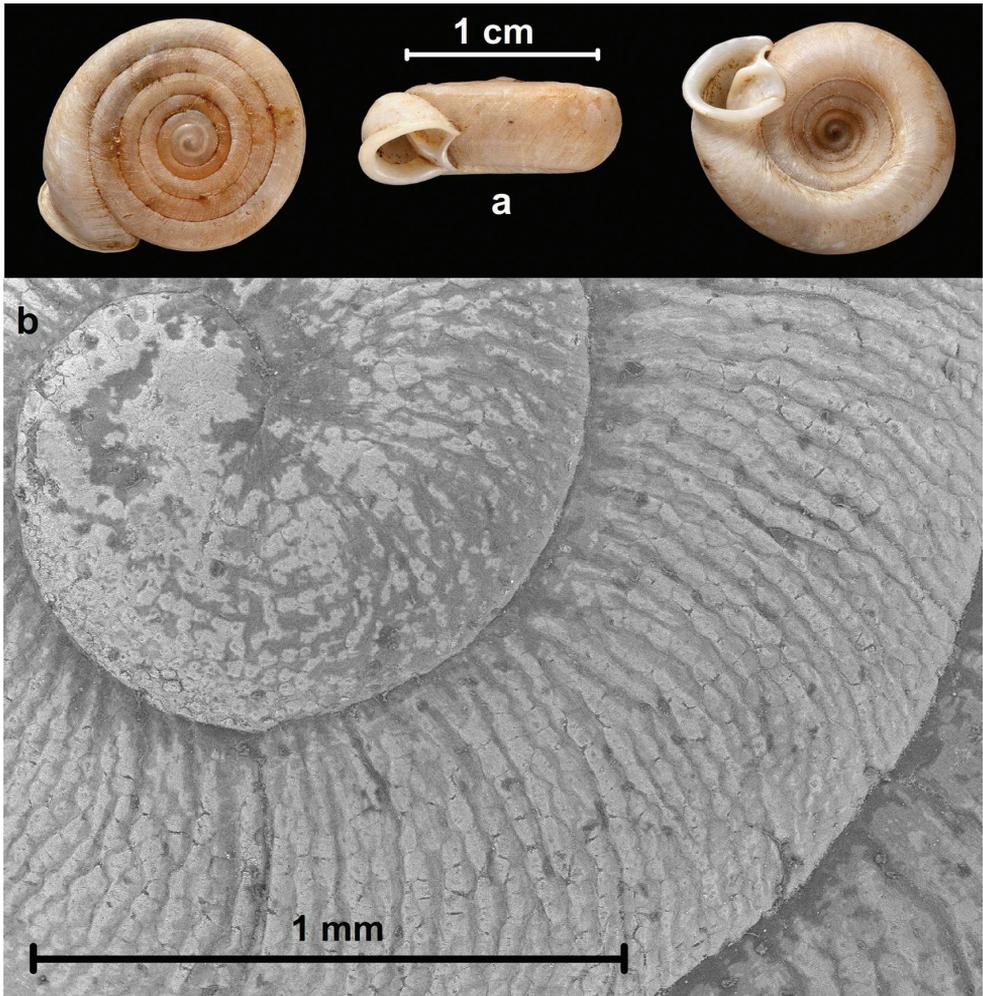
1999 *Chersaecia*, — Schileyko: Treatise on Recent Terrestrial Pulmonate Molluscs, Part 4. (...): 2: 462.

**Type species.** *Helix* (*Plectopylis*) *Leiophis* Benson, 1860 (Figure 2) by original designation.

**Diagnosis.** Shell sinistral or dextral, flat, widely umbilicated; in most cases protoconch seemingly “smooth” to the naked eye, but not glossy, rather matt; under the microscope usually tubercles of various size are visible (Figure 2B); sometimes the tuberculated protoconch is irregularly wrinkled; flat periostracal filaments are visible on the body whorl or on the dorsal surface in only a few species; aperture always with a fold; parietal wall with one vertical lamella and usually one or two long horizontal plicae (main plica and lower plica) reaching the callus; palatal plicae horizontal, sometimes divided in the middle, in some species with several additional denticles posteriorly, in some species similar to that of *Plectopylis* (three horizontal plicae above and one below the vertical plate formed by the accretion of two plicae).

Only one *Chersaecia* species is known anatomically (*Ch. simplex* in the original description: Solem 1966). Penis internally with approximately eight longitudinal rows, those situated next to the vas deferens are distinctly larger; vas deferens becomes a part of the penis wall at the penioviducal angle; no epiphallic differentiation observed; retractor muscle inserts on the dorsal surface of the penis and attaches to the diaphragm; diverticulum absent, gametolytic sac long and thickened.

**Differential diagnosis.** *Chersaecia* differs from *Endothyrella*, *Gudeodiscus* Páll-Gergely, 2013, *Halongella* Páll-Gergely, 2013, *Sicradiscus* Páll-Gergely, 2013 and *Sinicola* by the usually tuberculated (not regularly ribbed) protoconch. The presence of long parietal plicae (main and lower) distinguishes most *Chersaecia* species from most *Endothyrella*, *Gudeodiscus*, *Halongella*, *Sicradiscus* and *Sinicola* species. The delimitation



**Figure 2.** Shell (A) and protoconch (B) of *Chersaacia leiophis* (Benson, 1860), Akouktoung, purchased of W. Theobald Esq., NHMUK 1888.12.4.1526–1528 (two different shells). Photos: H. Taylor (A) and B. Páll-Gergely (B).

of *Chersaacia* from *Plectopylis* and *Endoplion* needs further investigation. Among all plectopylids examined to date *Chersaacia simplex* is the only species found to lack an epiphallus. The anatomy of more *Chersaacia* species should be studied to check the taxonomic value of the lack of the epiphallus.

**Content.** *austeni*, *brachydiscus*, *degerbolae*, *dextrorsa*, *kengtungensis*, *leiophis* (*pseudophis* is probably a synonym, see Gude 1908a), *muspratti*, *nagaensis*, *perarcta*, *perrieriae*, *refuga*, *shanensis*, *shiroiensis*, *simplex*.

**Distribution.** The genus is known to inhabit northeastern India, eastern and southern Myanmar (Burma) and northern Thailand.

**Genus *Endothyrella* Zilch, 1960**

1899c *Endothyra* (section of the genus *Plectopylis*) Gude: Science Gossip, 6: 148., non *Endothyra* Phillips, 1845 (Foraminifera).

1960 *Plectopylis* (*Endothyrella*), — Zilch: Handbuch der Paläozoologie, 6 (2).

1999 *Endothyrella*, — Schileyko: Treatise on Recent Terrestrial Pulmonate Molluscs, Part 4.(...): 2: 460.

**Type species.** *Helix plectostoma* Benson, 1836, by original designation.

**Diagnosis.** Shell sinistral or dextral; protoconch usually finely, regularly ribbed (see also discussion and Figures 6A–F); periostracal folds usually present on the body whorl; they are arranged in 3–7 lines; folds hair-like in most species, resulting from the rolling of flat folds; folds flat (not rolled) in some species only (see Figures 8D, 20A–F); dorsal sculpture strong, usually reticulated (both radial and spiral lines present, see Figure 8A); umbilicus wide to narrow; body whorl rounded in some species but rather bluntly shouldered (keeled) in others; apertural fold always absent; main plica usually absent (present in a few species only); low plica (if present) runs close to and parallel with the lower suture, it is usually very short (present only under the lamella), but in some species it reaches the callus; parietal wall with a single lamella with denticles posteriorly (probably homologous with the posterior lamella); two lamellae were reported in one species (*E. aborensis*) only; palatal plicae complicated in most species with many small denticles at their posterior ends; in many species they are at least partly divided in the middle.

Genitalia (see Figures 18, 21, 22B–F, 25, 26): The left ommatophoral retractor passes between penis and vagina (in sinistral species). Penis internally with hollows (small pocket-like structures) having calcareous granules inside; penial papilla absent; epiphallus may be longer than penis and enters penis laterally; epiphallus with longitudinal folds internally; small penial caecum usually present at the penis-epiphallus boundary; retractor muscle inserts on the caecum and attaches to the diaphragm; diverticulum (if present) and gametolytic sac are of the same size.

Radula (see Figures 19A–F): Central tooth larger than the ectocones of the first laterals; marginals tricuspid (= ectocones are divided) or even quadricuspid (both the endocones and ectocones are divided); the incision between the ectocones and endocones usually deep (*E. fultoni* has rhomboid marginals which are unique in the whole family).

**Differential diagnosis.** All known species of the genera *Sinicola*, *Gudeodiscus*, *Halongella* and *Sicradiscus* are dextral. Regardless of the coiling direction, most *Endothyrella* species differ from *Sinicola* by the presence of usually hair-like periostracal folds standing in multiple lines. Deciduous periostracal folds in *Sinicola* are present only along the keel and the folds are always flat. Most *Sinicola* species (especially the large species) have a sharp keel, whereas *Endothyrella* species usually have a rounded or slightly keeled, shouldered body whorl. The palatal plicae of *Sinicola* are usually simple, horizontal, straight and parallel, but in *Endothyrella* they are often oblique

to vertical, divided and ornamented with minute denticles at their posterior ends. In *Sinicola* the posterior lamella is present on the parietal wall, with two horizontal plicae anteriorly above and below, whereas in most *Endothyrella* species (probably except for *E. aborensis*) the anterior lamella is present and the posterior is missing or reduced to one or two short vertical plicae.

Some *Gudeodiscus* and *Halongella* species possess low, radial periostracal folds (e.g. Páll-Gergely et al. 2015, fig. 10e–f), similar to those of *E. nepalica* sp. n. (see there). The radial folds have serrated edges in *Gudeodiscus phlyarius* (Mabille, 1887). The tiny tips of the serrated folds seem to occur in a spiralling pattern (see Páll-Gergely and Hunyadi 2013, fig. 113 and Páll-Gergely et al. 2015, fig. 10c–d). All of these periostracal features of *Gudeodiscus* and *Halongella* are, however, easily distinguishable from the long, hair-like folds of the genus *Endothyrella*.

Some *Gudeodiscus* species possess a fold in the aperture, which is always missing in *Endothyrella*. The palatal plicae in *Gudeodiscus* are usually depressed Z- or L-shaped and posterior small denticles are very rare (except for one denticle above the posterior end of the last plica), whereas the palatal plicae of *Endothyrella* are frequently divided in the middle and posterior small denticles are usually present. In *Endothyrella* the anterior lamella is present, and often the upper horizontal plica is missing, whereas in *Gudeodiscus* both lamellae, or only the posterior one, are visible and the upper horizontal plica (above the lamella) is almost always present. Additionally, *Gudeodiscus* species have a rounded body whorl, while in many *Endothyrella* species the body whorl is angled or shouldered. Our limited knowledge on the anatomy of *Endothyrella* species shows that the entire inner penial wall of *Endothyrella* is covered by pits, whereas in *Gudeodiscus* these pocket-like structures are restricted to the a certain (usually apical) portion of the penis.

*Sicradiscus* is similar to *Endothyrella* in possessing a weak or reduced posterior lamella. Long periostracal folds standing in more than one row have also been found in one *Sicradiscus* species, namely in juveniles of *Sicradiscus transitus* Páll-Gergely, 2013. This species, however, has hairs standing in two spiral lines on the body whorl, whereas in *Endothyrella* the hairs are arranged in 3–7 spiral lines. This trait seems to be absent in adult *S. transitus* shells and all other species of *Sicradiscus*, but is common in fully grown *Endothyrella* shells (i.e. most species possess them). The two genera (i.e. *Endothyrella* and *Sicradiscus*) differ in the short, straight palatal plicae, which are usually connected in *Sicradiscus* vs. longer, more complex palatal plicae sometimes having additional denticles in *Endothyrella*. In both genera divided plicae may occur, but in the case of *Sicradiscus* the posterior fourth and fifth plicae seem to be always connected, whereas in *Endothyrella* all plicae are free. Moreover, western *Sicradiscus* species (*feheri* Páll-Gergely, 2013, *invius* [Heude, 1885], *mansuyi* [Gude, 1908b], *securus* [Heude, 1885] and *transitus*) differ from *Endothyrella* by the presence of a strong apertural fold.

*Plectopylis* and *Endoplion* species have a granulated or smooth protoconch, whereas it is usually finely ribbed in *Endothyrella*. Moreover, *Plectopylis* and *Endoplion* usually have a strong apertural fold which is often connected to a long main plica. In contrast, although some *Endothyrella* species have a main plica, they all lack an apertural fold. See also under *Chersaecia* and Table 3.

**Table 3.** Characters of the plectopylid genera possessing ribbed protoconchs.

Genus	Coiling direction	Apertural fold	Lower plica	Body whorl	Anterior lamella	Posterior lamella	Periostracal folds	Penial pockets
<i>Endothyrella</i>	sinistral or dextral	absent	short or long (reaching peristome)	rounded or keeled	present	present (?), absent or reduced	usually in multiple rows	whole penial wall
<i>Sinicola</i>	dextral	absent (present in 1 species)	short	keeled	absent or reduced	present	present in a single row or absent	whole penial wall
<i>Gudeodiscus</i>	dextral	absent or present	missing or short	rounded	present, reduced or absent	present	absent	apical part
<i>Halongella</i>	dextral	present	short	rounded	present, reduced or absent	present	absent	whole penial wall
eastern <i>Sicradiscus</i>	dextral	absent	missing or short	keeled	present	present or reduced	present in a single row or absent	whole penial wall
western <i>Sicradiscus</i>	dextral	present	missing or short	rounded	present	present or reduced	absent	apical part

**Content.** *aborensis*, *affinis*, *angulata* sp. n., *babbagei*, *bedfordi*, *blanda*, *brahma*, *dolakhaensis* sp. n., *fultoni*, *inexpectata* sp. n., *macromphalus* (syn.: *gregorsoni*), *minor*, *mirienseis*, *nepalica* sp. n., *oakesi*, *oglei*, *pinacis*, *plectostoma*, *robustistriata* sp. n., *serica* (syn: *munipurensis*), *sowerbyi*, *tricarinata*, *williamsoni*. See also Tables 4 and 5.

**Distribution.** The distribution of this genus is restricted to Nepal, northeastern India and the province Sichuan in China. One species (*E. plectostoma*) was reported from Myanmar (Figure 3).

## Dextral species

### *Endothyrella babbagei* (Gude, 1915)

Figures 4A, 6C

1915 *Plectopylis* (*Sinicola*) *babbagei* Gude: Records of the Indian Museum, 8: 512–513, Plate 42, figs 4a–d. [“Luyor Peak, Abor Hills, alt. 7200 ft. Lat. 28°45': Long. 95°45'"].

1920 *Plectopylis* (*Sinicola*) *babbagei*, — Gude: Proceedings of the Malacological Society of London, 14 (2–3): 64.

2013 *Endothyrella babbagei*, — Páll-Gergely & Hunyadi: Archiv für Molluskenkunde, 142 (1): 5.

**Types.** Peak Luyor, Abor Hills, 7,200 ft, leg. C.F.G. Oakes R.E., NHMUK 1903.7.1.3529. (holotype, Figures 4A, 6C).



**Figure 3.** Known distribution of the genus *Endothyrella* Zilch, 1960.



**Figure 4.** Shells of *Endothyrella* species. **A** *Endothyrella babbagei* (Gude, 1915), NHMUK 1903.7.1.3529 (holotype) **B** *Endothyrella inexpectata* Páll-Gergely, sp. n., NHMUK 20140023 (holotype). Photos: H. Taylor (**A**) and B. Páll-Gergely (**B**). Scale represent 5 mm.

**Table 4.** (Sub)generic classification of *Endothyrella* Zilch, 1960 (formerly *Endothyra* Gude, 1899) species by previous authors. Species marked with a star were moved to *Endothyrella* by Páll-Gergely & Hunyadi (2013). Abbreviations: n. m.: not mentioned.

Name	Subgenus in Gude (1899c)	Subgenus in Gude (1915)
<i>aborensis</i> *		<i>Endoplön</i>
<i>affinis</i>	<i>Endothyra</i>	n. m.
<i>babbagei</i> *		<i>Sinicola</i>
<i>bedfordi</i>		<i>Chersaecia</i>
<i>blanda</i>	<i>Endothyra</i>	n. m.
<i>brahma</i>	<i>Chersaecia</i>	<i>Chersaecia</i>
<i>exerta</i> (syn. of <i>tricarinata</i> )	<i>Endothyra</i>	n. m.
<i>fultoni</i>	<i>Endothyra</i>	n. m.
<i>gregorsoni</i> (syn. of <i>macromphalus</i> )		<i>Endothyra</i>
<i>hanleyi</i>	<i>Endothyra</i>	n. m.
<i>macromphalus</i>	<i>Endothyra</i>	<i>Endothyra</i>
<i>minor</i>	<i>Endothyra</i>	n. m.
<i>miriensis</i>		<i>Endothyra</i>
<i>municipurensis</i> (syn. of <i>serica</i> )	<i>Chersaecia</i>	n. m.
<i>oakesi</i>		<i>Endothyra</i>
<i>oglei</i>	<i>Chersaecia</i>	n. m.
<i>pinacis</i>	<i>Endothyra</i>	<i>Endothyra</i>
<i>plectostoma</i>	<i>Endothyra</i>	n. m.
<i>serica</i>	<i>Chersaecia</i>	n. m.
<i>sowerbyi</i>	<i>Endothyra</i>	n. m.
<i>tricarinata</i>	<i>Endothyra</i>	n. m.
<i>williamsoni</i>		<i>Chersaecia</i>

**Diagnosis.** Shell small, dextral, slightly concave above; widely umbilicated; hairs arranged in three spiral lines on the body whorl; callus strong, palatal plicae short, simple, parietal wall with a single curved lamella.

**Measurements** (in mm): D: 14.4, H: 6.3 (n = 1).

**Differential diagnosis.** For differences with *E. oglei*, and *E. serica* and *E. inexpectata* sp. n., see there. See also Table 5.

**Distribution.** Only known from the type locality (Figure 7).

***Endothyrella inexpectata* Páll-Gergely, sp. n.**

<http://zoobank.org/183E6262-0DD8-4881-BBFC-61F608546481>

Figures 4B, 6F, 8D, 9A–B

**Type material.** China, Sichuan Sheng (四川省), Panzihua Shi (攀枝花市), Yanbian Xian (盐边县), Qinghe Xiang (箐河乡), Qinghepubu (箐河瀑布), Xianrendong (仙人洞), 1410 m, 27°03.834'N, 101°23.611'E, leg. Hosoda, T., Ohara, K., Okubo,

**Table 5.** Main diagnostic characters of *Endothyrella* species.

Species	Diagnostic characters	Similar species (most similar species in bold)
<i>aborensis</i>	depressed Z-shaped palatal plicae; two parietal lamellae (?)	
<i>affinis</i>	narrow umbilicus; four hair rows; horizontal parietal plica absent	<b><i>plectostoma</i></b> , <i>sowerbyi</i> , <i>tricarinata</i>
<i>angulata</i> sp. n.	body whorl shouldered; four hair rows	<i>dolakhaensis</i> sp. n., <i>pinacis</i> , <i>minor</i>
<i>babbagei</i>	dextral shell; flattened dorsal side; 14 mm	<b><i>inexpectata</i> sp. n.</b> , <i>oglei</i> , <i>serica</i>
<i>bedfordi</i>	single parietal lamella with long lower plica; posterior ends of palatal plicae with several additional small denticles	
<i>blanda</i>	conical dorsal side; 7 hair rows	<i>macromphalus</i> , <i>minor</i> , <i>robustistriata</i> sp. n., <b><i>williamsoni</i></b>
<i>brahma</i>	three parallel, horizontal parietal plicae anterior to the lamella	
<i>dolakhaensis</i> sp. n.	rather conical dorsal side; slightly angulated body whorl; 5 hair rows	<i>angulata</i> sp. n., <i>sowerbyi</i>
<i>fultoni</i>	large size (19.9–20.3 mm); reversed trapezoid shell shape	
<i>inexpectata</i> sp. n.	dextral shell; flattened dorsal side; 6.6–6.7 mm	<b><i>babbagei</i></b> , <i>oglei</i> , <i>serica</i>
<i>macromphalus</i>	nearly flat dorsal side; smooth ventral side	<i>blanda</i> , <b><i>minor</i></b> , <b><i>robustistriata</i> sp. n.</b> , <i>williamsoni</i>
<i>minor</i>	flat dorsal side; four hair rows	<i>blanda</i> , <b><i>macromphalus</i></b> , <b><i>robustistriata</i> sp. n.</b> , <i>williamsoni</i>
<i>miriensis</i>	prominent spiral sculpture	
<i>nepalica</i> sp. n.	hairless shell; domed dorsal side; rounded body whorl; simple palatal plicae	<i>oakesi</i> , <i>pinacis</i>
<i>oakesi</i>	hairless shell; slightly domed dorsal side; rounded body whorl; complicated palatal plicae	<i>nepalica</i> sp. n., <i>pinacis</i>
<i>oglei</i>	dextral shell; 16.8–16.9 mm; protoconch without groove	<i>babbagei</i> , <i>inexpectata</i> sp. n., <b><i>serica</i></b>
<i>pinacis</i>	hairless shell; slightly elevated dorsal side; shouldered body whorl; simple palatal plicae	<i>nepalica</i> sp. n., <i>oakesi</i>
<i>plectostoma</i>	very narrow umbilicus; five hair rows; horizontal parietal plica present	<b><i>affinis</i></b> , <i>sowerbyi</i> , <i>tricarinata</i>
<i>robustistriata</i> sp. n.	elevated spire; smooth ventral side; strongly reticulated dorsal surface	<i>blanda</i> , <b><i>macromphalus</i></b> , <i>minor</i> , <i>williamsoni</i>
<i>serica</i>	dextral shell; protoconch with groove	<i>babbagei</i> , <i>inexpectata</i> sp. n., <b><i>oglei</i></b>
<i>sowerbyi</i>	narrow umbilicus; thin peristome; five hair rows; weak horizontal parietal plica	<i>affinis</i> , <i>dolakhaensis</i> sp. n., <b><i>plectostoma</i></b> , <i>tricarinata</i>
<i>tricarinata</i>	very narrow umbilicus; shouldered whorls; four hair rows	<b><i>affinis</i></b> , <b><i>plectostoma</i></b> , <b><i>sowerbyi</i></b>
<i>williamsoni</i>	conical dorsal side; hairless shell; long horizontal parietal plica	<b><i>blanda</i></b> , <b><i>macromphalus</i></b> , <i>minor</i> , <i>robustistriata</i> sp. n.

K., Otani, J. U., 12.09.2013, NHMUK 20140023 (holotype, Figures 4B, 6F, 8D, 9A–B), JUO/1 (paratype), TH/1 (paratype = juvenile shell); China, Sichuan Sheng (四川省), Liangshan Yizu Zizhizhou (凉山彝族自治州), Yanyuan Xian (盐源县), Bainiao Zhen (白鸟镇), Kedengrongdong (柯登溶洞) (cave), 2620 m, 27°43.103'N, 101°31.021'E, leg. Hosoda, T., Ohara, K., Okubo, K., Otani, J. U., 13.09.2013, JUO/1 juvenile shell (not paratype); Sichuan Sheng (四川省), Liangshan Zhou (凉山州), Yanyuan Xian (盐源县), Baiwu Zhen (白鸟镇), eastern edge of Kedeng Cun (柯登村), 2640 m, 27°43.897'N, 101°31.208'E, leg. Hunyadi, A., Szekeres, M., 11.06.2015., HA/1 paratype.

**Diagnosis.** Shell very small, dextral, almost flat, relatively widely umbilicated with elevated callus; hairs standing in three lines on the body whorl; parietal wall with a single, curved lamella; palatal wall with six short plicae.

**Description.** Shell dextral, with almost flat, very slightly domed dorsal side (protoconch slightly elevates from the dorsal surface); brownish or slightly reddish in colour; protoconch consists of 1.5–1.75 whorls, first whorls rather smooth, last 0.25–0.5 whorl regularly ribbed (Figure 6F); teleoconch with irregular, rough growth lines and spiral structure; sculpture stronger on the dorsal surface but still well-visible on the ventral surface; deciduous, slim and flat folds standing in three lines on the body whorl (Figure 8D); whorls 4.75, very much bulging, separated by deep suture; umbilicus moderately wide and deep; apertural lip whitish, thickened and slightly reflexed; callus strong, elevated, sharp and slightly S-shaped; with canals at both ends; no fold in the aperture.

One specimen (the holotype) was opened. The armature is situated very close to the aperture, palatal plicae visible from oblique view through the aperture. Parietal wall with a single curved lamella without additional denticles; arms of the lamella pointing posteriorly; palatal wall with six very short plicae becoming narrower posteriorly; the last one with an additional denticle posteriorly (Figures 9A–B).

**Measurements** (in mm): D: 6.6–6.7, H: 3.0–3.1 (n = 2, from different localities).

**Differential diagnosis.** *Endothyrella babbagei* is much larger than *E. inexpectata* sp. n., and it has flatter whorls and has a weaker callus than the new species. *Sinicola* species of the same size have a keeled or shouldered body whorl and have two parallel parietal plicae anterior to or above the lamella (one near the upper, the other near the lower suture). *Sicradiscus invius* also occurs in Sichuan, but it is smooth (glossy) and has a strong apertural fold. See also under *Endothyrella oglei* and *E. serica* and Table 5.

**Etymology.** The name *inexpectata* (meaning unexpected in Latin) refers to the surprising new, especially dextral *Endothyrella* species in China.

**Type locality.** Sichuan Sheng (四川省), Panzhihuashi (攀枝花市), Yanbian Xian (盐边县), Qinghe Xiang (箐河乡), Qinghepubu (箐河瀑布), Xianrendong (仙人洞), 1410 m, 27°03.834'N, 101°23.611'E.

**Distribution.** *Endothyrella inexpectata* sp. n. is known from two localities in western Sichuan province, China (Figure 7).

***Endothyrella oglei* (Godwin-Austen, 1879)**

Figures 5A, 6A

1879a *Helix* (*Plectopylis*) *Oglei* Godwin-Austen: Journal of the Asiatic Society of Bengal, 48 (2): 3, Plate 1, figs 2, 2a–c. [“Near Sadiya, Assam”].

1887 *Helix* (*Plectopylis*) *oglei*, — Tryon: Manual of Conchology..., 2 (3): 159, Plate 36, figs 29–31.

1898 *Plectopylis oglei*, — Gude: Science Gossip, 4: 263, figs 68a–h.

1899c *Plectopylis* (*Chersaecia*) *oglei*, — Gude: Science Gossip, 6: 148.

1899d *Plectopylis* (*Chersaecia*) *oglei*, — Gude: Science Gossip, 6: 175, 176.

1914b *Plectopylis* (*Chersaecia*) *oglei*, — Gude: The Fauna of British India...: 73, 92–93, figs 39a–h.

**Types.** Sadia, E. Assam, leg. Ogle, NHMUK 1903.7.1.740. (4 syntypes, Figure 5A, 6A).

**Diagnosis.** Shell middle sized, dextral, yellowish-reddish striped with moderately wide umbilicus and somewhat domed dorsal surface; callus strong, palatal plicae divided at their middle and the posterior fragments are connected by a ridge; parietal wall with a single curved lamella with posteriorly elongated upper and lower ends. Probably at least the upper elongation is homologous with the posterior denticle of other *Endothyrella* species.

**Measurements** (in mm): D: 16.8–16.9, H: 7.7–8.1 (n = 2, type series).

**Differential diagnosis.** *Endothyrella babbagei* and *E. inexpectata* sp. n. differ from the *E. oglei* by the flat dorsal surface of the shell and the presence of hairs arranged in three rows on the body whorl. See also under *E. serica* and Table 5.

**Remarks.** The information published by Gude (1914b) (major diameter 27, minor diameter 25 mm) is wrong; it probably refers to “*Chersaecia andersoni*”.

**Distribution.** The species is known from the type locality only (Figure 10).

***Endothyrella serica* (Godwin-Austen, 1875)**

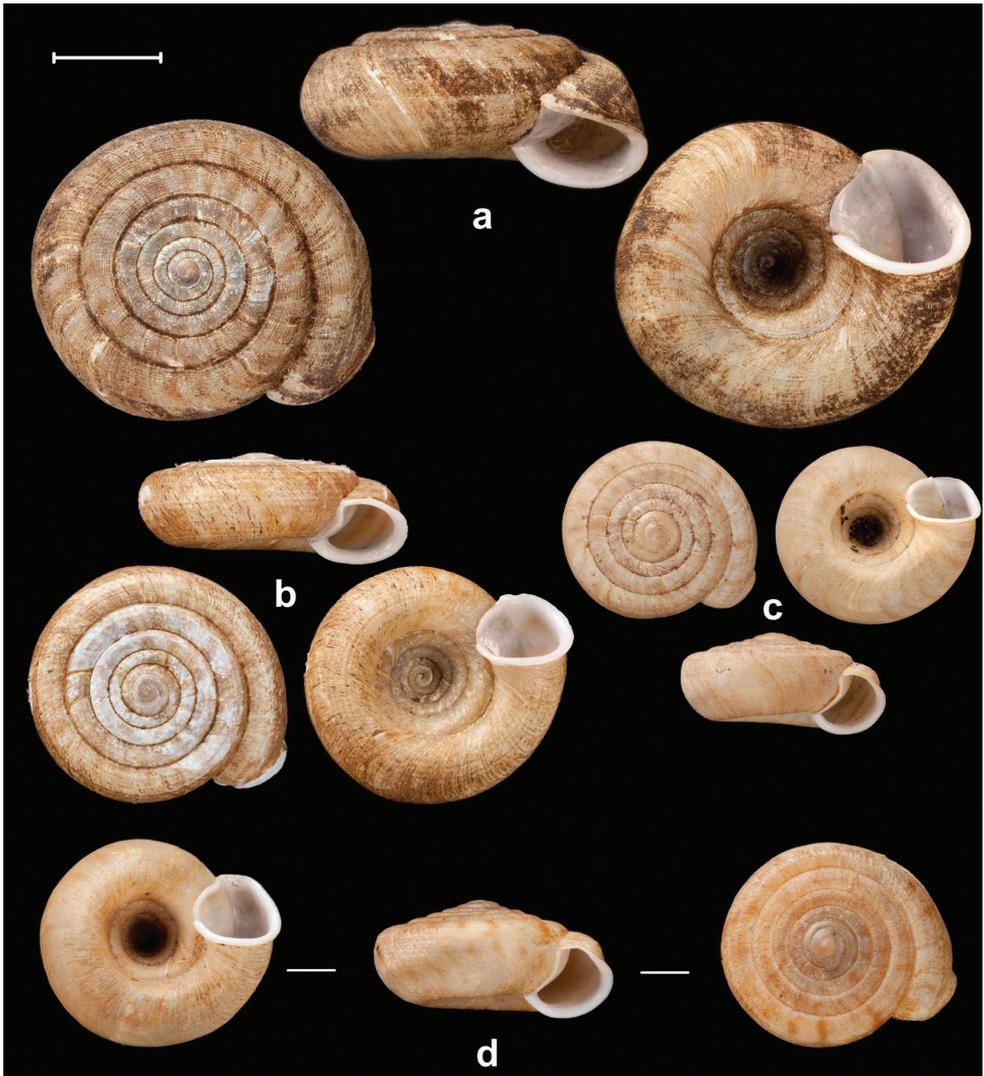
Figures 5B–D, 6B

1875 *Helix* (*Plectopylis*) *serica* Godwin-Austen: Proceedings of the Zoological Society of London: 608, 609, 612, Plate 73, figs 5a–c. [“on the peak of Henozdan, Burrail range” “above 5000 feet on the same range as far east as the Kopamedza ridge”] (1874, part IV, published in 1875; see Duncan 1937).

1875 *Helix* (*Plectopylis*) *municipurensis* Godwin-Austen **new synonym**: Proceedings of the Zoological Society of London: 610, 612, Plate 73, figs 6a–c. [“At the end of the Ihang valley, Muniপুর, at about 3000–4000 feet”] (1874, part IV, published in 1875; see Duncan 1937).

1875 *Helix sericata* (sic.), — Hanley & Theobald: Conchologia Indica...: 53, Plate 132, figs 8, 9.

1878 *Helix* (*Plectopylis*) *serica*, — Nevill: Hand list of Mollusca in the Indian Museum, Calcutta...: 71. [“Hengdan Peak and Burrail”].

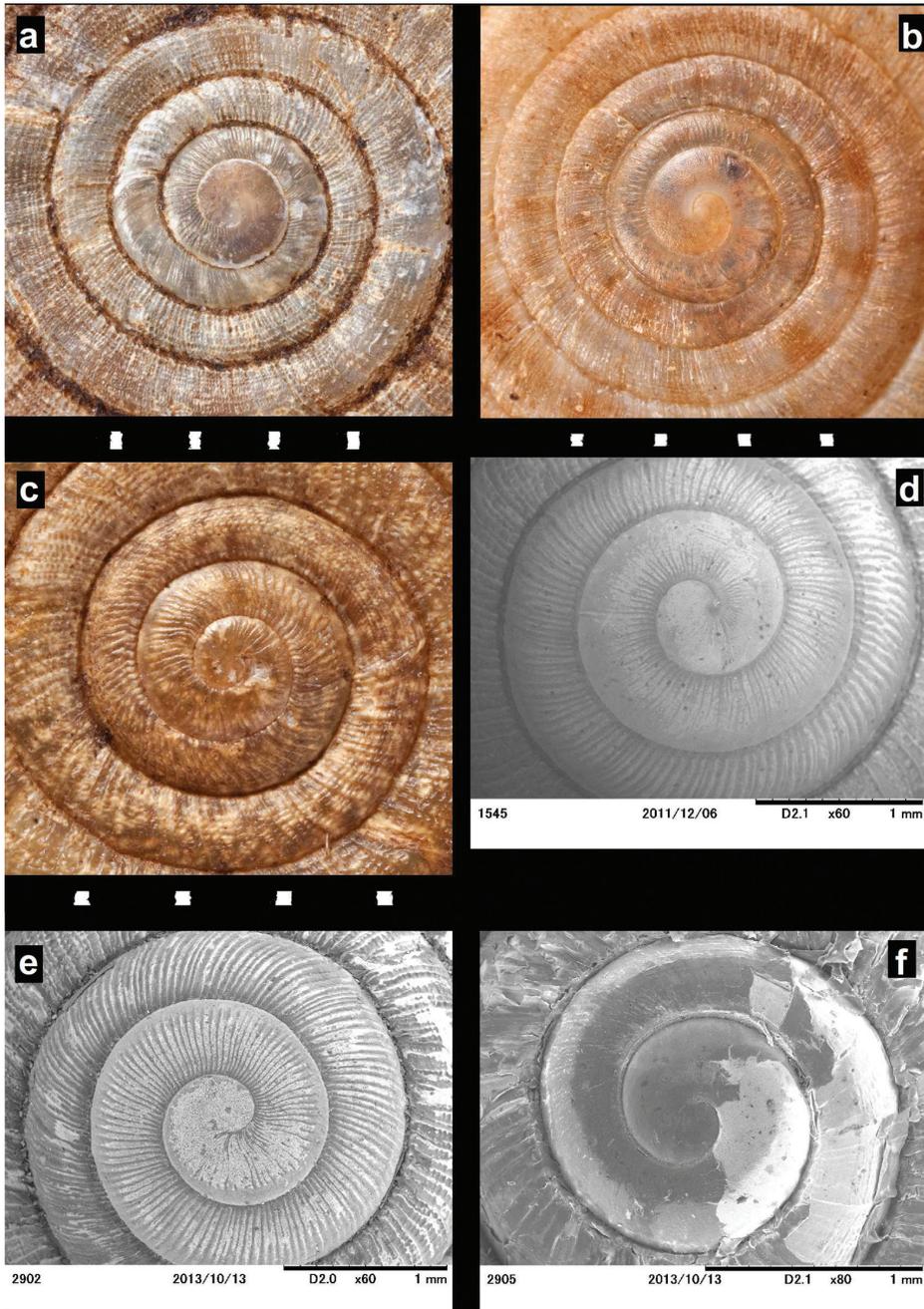


**Figure 5.** Shells of *Endothyrella* species. **A** *Endothyrella oglei* (Godwin-Austen, 1879), NHMUK 1903.7.1.740. (syntype) **B** *Endothyrella serica* (Godwin-Austen, 1875), NHMUK 1903.7.1.741 (syntype of *serica*) **C** *Endothyrella serica*, NHMUK 1903.7.1.744 (syntype of *serica*) **D** *Endothyrella serica*, NHMUK 1903.7.1.742. (syntype of *munipurensis*). All photos by Harold Taylor (NHMUK). Scale represent 5 mm.

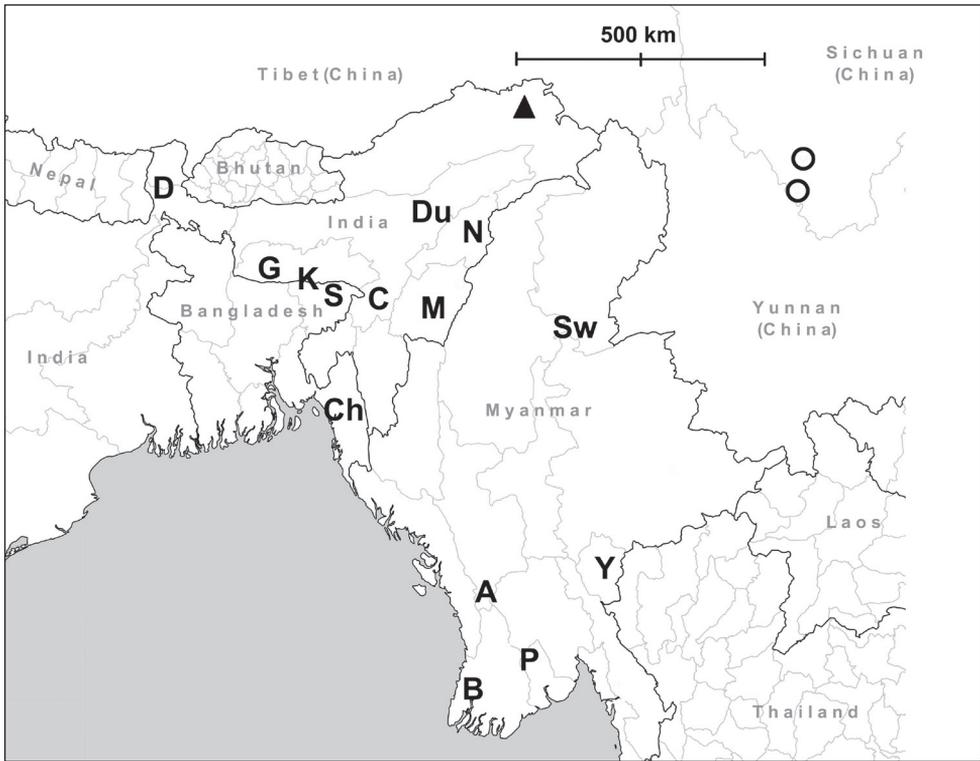
1879a *Helix (Plectopylis) serica*, — Godwin-Austen: Journal of the Asiatic Society of Bengal, 48 (2): 3.

1887 *Helix (Plectopylis) serica*, — Tryon: Manual of Conchology..., 2 (3): 159, Plate 34, figs 49–52.

1887 *Helix (Plectopylis) Munipurensis*, — Tryon: Manual of Conchology..., 2 (3): 160, Plate 34, figs 56–58.



**Figure 6.** Photos (A–C) and SEM images (D–F) of *Endothyrella* protoconchs. **A** *Endothyrella oglei* (Godwin-Austen, 1879), same data as in Fig. 5 **B** *Endothyrella serica* (syntype of *munipurensis*, same data as in Fig. 5.) **C** *Endothyrella babbagei* (Gude, 1915), same data as in Fig. 3 **D** *Endothyrella plectostoma* (Benson, 1836), MNHN 2012-27053 **E** *Endothyrella nepalica* Budha & Páll-Gergely sp. n., paratype from the Siddha Cave **F** *Endothyrella inexpectata* Páll-Gergely, sp. n., (holotype). **A–C** Harold Taylor **D–F** B. Páll-Gergely.



**Figure 7.** Distribution of *Endothyrella* species. Empty circle: *Endothyrella inexpectata* sp. n.; Filled triangle, top up: type locality of *Endothyrella babbagei*. Letters indicate localities of *Endothyrella plectostoma* (Benson, 1836). Abbreviations: **A** Arakan Hills **B** Bassein (= Patheingyi) **C** Silchar (Cachar) **Ch** Chittagong (Ghoramara) **D** Darjeeling **Du** Dunsiri valley **G** Garo Hills **K** Khasi Hills **M** Manipur **N** Naga Hills **P** Pegu (= Bago) **S** Sylhet **Sw** Shwegu **Y** Ywathit.

1897a *Plectopylis serica*, — Gude: Science Gossip, 3: 205–206, figs 31a–c.

1897 *Plectopylis serica*, — Gude: Science Gossip, 3: 246.

1898 *Plectopylis munipurensis*, — Gude: Science Gossip, 4: 263–264, figs 69a–g.

1899c *Plectopylis (Chersaecia) serica*, — Gude: Science Gossip, 6: 148.

1899c *Plectopylis (Chersaecia) munipurensis*, — Gude: Science Gossip, 6: 148.

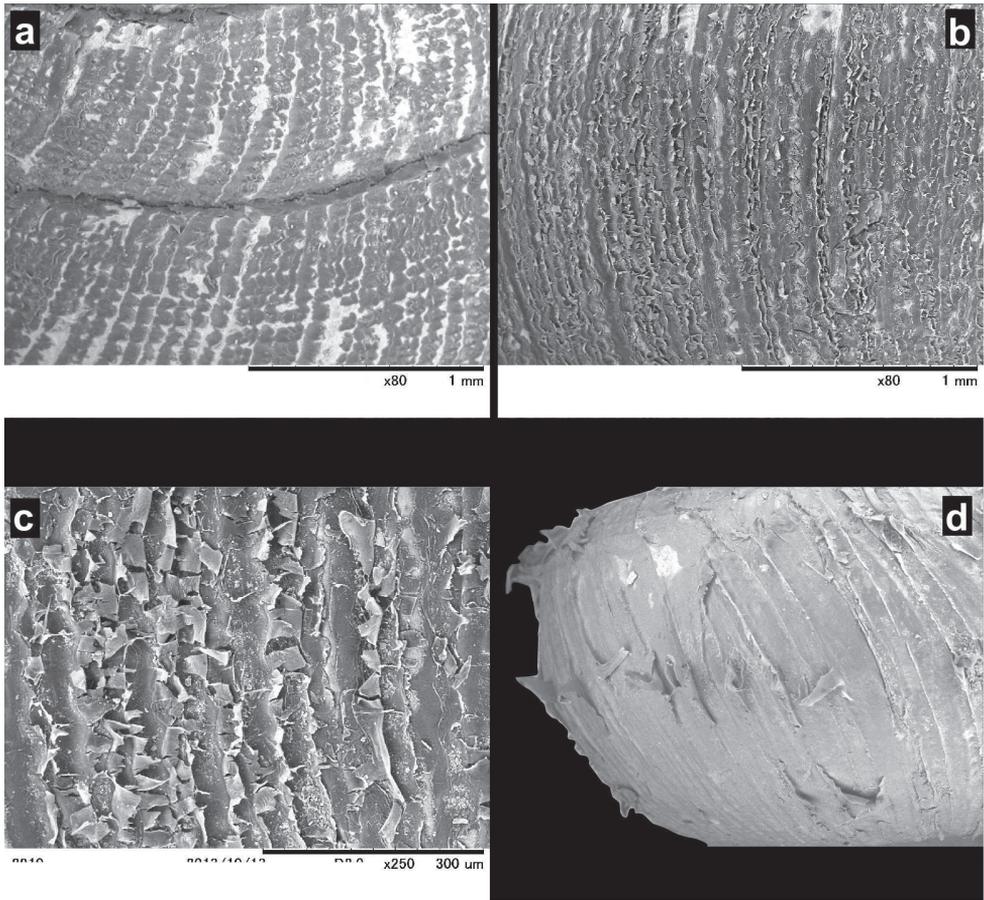
1899d *Plectopylis (Chersaecia) serica*, — Gude: Science Gossip, 6: 175, 177.

1899d *Plectopylis (Chersaecia) munipurensis*, — Gude: Science Gossip, 6: 175, 176.

1914b *Plectopylis (Chersaecia) serica*, — Gude: The Fauna of British India...: 73, 93–94, figs 40a–c.

1914b *Plectopylis (Chersaecia) munipurensis*, — Gude: The Fauna of British India...: 73, 94–95, figs 41a–g.

**Types.** Khunho, H.S. Naga Hills, leg. Godwin-Austen, NHMUK 1903.7.1.741 (8 syntypes of *serica*, Figure 5B); Hengdan P., Naga Hills, leg. Godwin-Austen, NHMUK

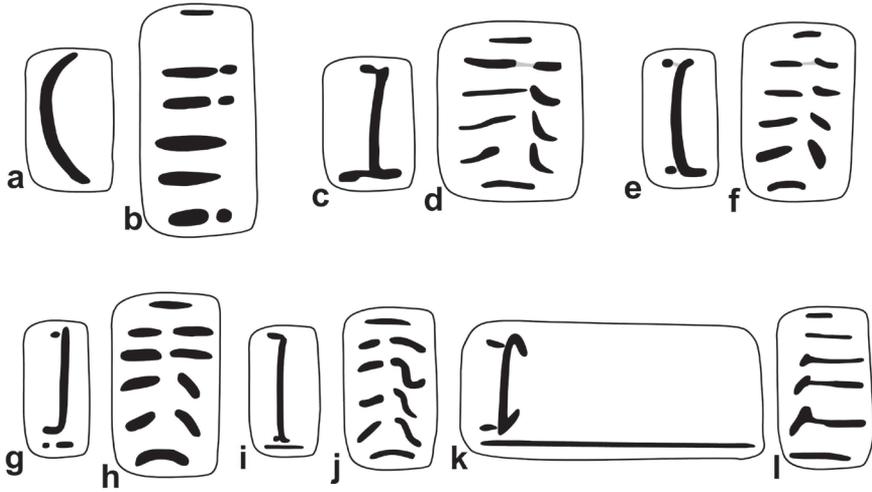


**Figure 8.** SEM images of *Endothyrella* shells. **A** *Endothyrella nepalica* Budha & Páll-Gergely, sp. n., 4<sup>th</sup>, 5<sup>th</sup> whorl, for locality see Fig. 6. **B** *Endothyrella nepalica* Budha & Páll-Gergely, sp. n. body whorl **C** *Endothyrella nepalica* Budha & Páll-Gergely, sp. n. body whorl **D** *Endothyrella inexpectata* Páll-Gergely, sp. n., body whorl (holotype). All images by B. Páll-Gergely.

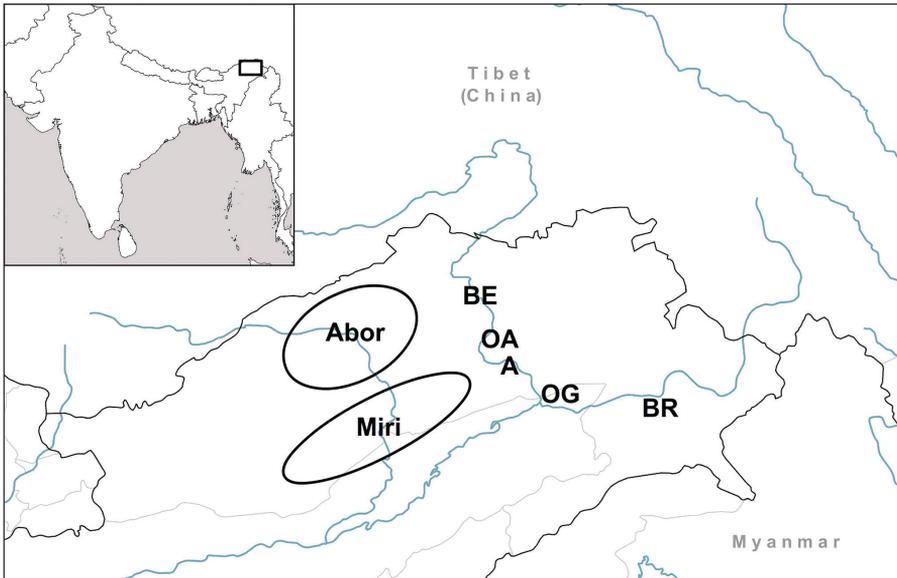
1903.7.1.744 (6 syntypes of *serica*, Figure 5C); Manipur Hills, head of the Ihang valley, Manipur, leg. Godwin-Austen, NHMUK 1903.7.1.742. (6 syntypes of *muniपुरensis*, Figure 5D).

**Additional material examined.** Naga Hills, coll. Godwin-Austen, NHMUK 1903.7.1.743/4 (under the name *muniपुरensis*); Japvo Peak, Nr. Kohima, Naga Hills, NHMUK 20150128/8; Lhota Naga, coll. Godwin-Austen, NHMUK 1903.7.1.745/6; no locality, leg. Maxwell, coll. Godwin-Austen, NHMUK 20150129/5; India, Hengdan Peak, NHMUK 1891.3.17.356–357/2; India, NHMUK 1874.4.26.2/2; Khasi Hills, coll. W. Blanford, NHMUK 1906.2.2.360/2.

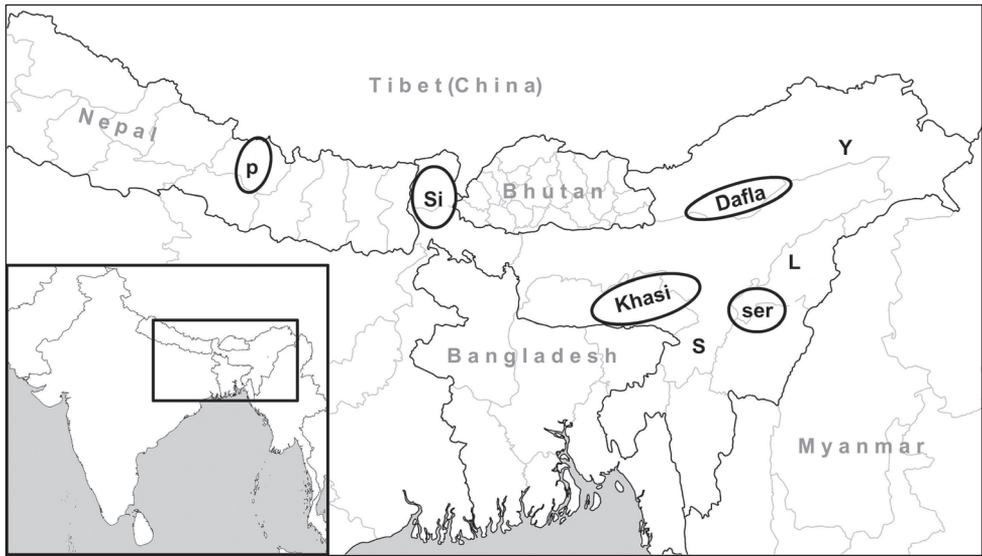
**Diagnosis.** Shell very small to small, dextral, yellowish-reddish striped with moderately wide umbilicus and depressed conical dorsal surface; callus strong, palatal plicae more or less straight, simple or have dichotomously divided posterior ends; parietal



**Figure 9.** Parietal (**A, C, E, G, I, K**) and palatal (**B, D, F, H, J, L**) lamellation of *Endothyrella* spp. **A–B** *Endothyrella inexpectata* sp. n. (holotype) **C–D** *Endothyrella nepalica* sp. n., for locality, see Fig. 6. **E–F** *Endothyrella nepalica* sp. n., shell from Mahadevsthan **G–H** *Endothyrella dolakhaensis* sp. n., shell from the type locality **I–J** *Endothyrella angulata* sp. n., shell from the type locality **K–L** *Endothyrella robustistriata* sp. n., NHMUK 1903.7.1.767 (two different specimens). Outer view: **B, L**; inner view: **D, F, H, J**. Diagrammatic.



**Figure 10.** Distribution of *Endothyrella* species in Northeastern India. Abbreviations: **A** type locality of *Endothyrella aborensis* (Gude, 1915); **Abor** Abor Hills (type locality of *Endothyrella williamsoni* (Gude, 1915) **BE** type locality of *Endothyrella bedfordi* (Gude, 1915) **BR** Type locality of *Endothyrella brahma* (Godwin-Austen, 1879); **Miri** Miri Hills (type locality of *Endothyrella miriensis* (Gude, 1915) **OA** Type locality of *Endothyrella oakesi* (Gude, 1915) **OG** Type locality of *Endothyrella oglei* (Godwin-Austen, 1879).



**Figure 11.** Distribution of *Endothyrella* species in Northeastern India. Abbreviations: **Dafla** Dafla Hills (locality of *E. macromphalus*); **Khasi** Khasi Hills (locality of *E. affinis*, *E. fultoni*, *E. robustistriata* sp. n., *E. macromphalus*, *E. minor* and *E. tricarinata*), **L** Lhota Naga (locality of *E. robustistriata* sp. n.) **P** Nepalese localities of *E. minor* **SER** *Endothyrella serica* (Godwin-Austen, 1875) **S** Silchar (locality of *E. blanda*) **SI** Sikkim (locality of *E. blanda*, *E. minor*, *E. pinacis*) **Y** Yamne valley (type locality of *Plectopylis gregorsoni*).

wall with a single curved lamella with denticles near the upper and lower ends posteriorly, which occasionally fuse with the lamella.

**Measurements** (in mm): D: 9.7–9.9, H: 4.4–4.8 (n = 3, NHMUK 1903.7.1.744); D: 9.9–13, H: 4.9–5.5 (n = 4, NHMUK 1903.7.1.741); D: 10.9–11.7, H: 5.1–5.7 (n = 3, NHMUK 1903.7.1.742).

**Differential diagnosis.** *Endothyrella babbagei* and *E. inexpectata* sp. n. differ from *E. serica* by the flat dorsal surface of the shell and the presence of three rows of hairs on the body whorl. *Endothyrella oglei* differs from the also dextral *E. serica* by the much larger size, the absence of the groove on the protoconch, which runs parallel with the suture in *E. serica*, and the morphology of the lamella which has only posteriorly elongated ends. See also Table 5.

**Distribution.** The species is recorded from the Naga Hills (see also remarks). “*Plectopylis munipurensis*” was described from “end of the Ihang valley” (Figure 11).

**Remarks.** Godwin-Austen (1875) described *Helix (Plectopylis) serica* and *Helix (Plectopylis) munipurensis* in the same publication. He did not mention the differences between the two species. According to the illustrations and the identification key in the original description, the upper end of the lamella in *munipurensis* is more elongated anteriorly than that of *H. serica*. Two shells of *E. serica* were opened from the Hengdan sample, and both had an anteriorly elongated plica. In this respect, and also in shell shape, these shells were more similar to *E. munipurensis* specimens. In the Khunho sample four shells were opened, three having no or very slight upper elongation, but one

had an as long plica as in typical *munipurensis* shells. Examining the type specimens of the two species we have not found significant differences. The width of the umbilicus and the height of the spire showed some variability. Therefore we synonymize *munipurensis* with *serica*. We choose *Helix (Plectopylis) serica* to be the valid specific name.

In the original description Godwin-Austen (1875) reported the species from the “peak of Henozdan” and from the “Kopamedza ridge”. The second sample is probably identical with the one from Khunho in the type collection of the NHM.

Gude (1897h) mentions that according to Godwin-Austen, the correct names for “Henozdan” and “Kopameda” in Gude (1897a) are “Hengdan” and “Kopamedza”, respectively. According to the same erratum, Godwin-Austen also mentioned that the locality of Ponsonby’s shell (Sylhet) is probably incorrect, because *Plectopylis serica* is a very local species, inhabiting altitudes higher than 5000 feet.

### Sinistral species

#### *Endothyrella aborensis* (Gude, 1915)

Figure 12

- 1915 *Plectopylis (Endoplion) aborensis* Gude: Records of the Indian Museum, 8: 511–512, Plate 42, Fig. 3a–d. [“Between Renging and Rotung, 2200 ft., Abor country.”].  
 2013 *Endothyrella aborensis*, — Páll-Gergely & Hunyadi: Archiv für Molluskenkunde, 142 (1): 5.

**Types.** According to the original description, two shells, an adult and a juvenile were collected and finally deposited in the Indian Museum (inventory numbers: 5998 and 6135). Specimen reference collections in the Indian Museum were transferred to the ZSI following foundation of the ZSI in 1916. The ZSI supplied us with two photos of an adult shell under the name of *Plectopylis aborensis*, which they considered as one of the type specimens. These photos, however, clearly showed a different specimen than the one figured in Gude (1915). No other information could be obtained from the ZSI.

**Diagnosis.** Shell small, sinistral, almost flat, widely umbilicated; callus strong; palatal plicae Z or L-shaped; there are two parietal lamellae, a short upper plica which is in contact with the posterior lamella, and a long lower plica which reaches the peristome.

**Measurements** (in mm): D: 14, H: 6.5 (according to the original description).

**Differential diagnosis.** The species was not examined by us, but according to the original description the species differs from all congeners by the short and uniquely shaped palatal plicae, which are depressed Z-shaped, or the lower branch of the “Z” is elongated. See also Table 5.

**Distribution.** Known from the type locality only (approximately 28°10'N, 95°13'E) (Figure 10).

**Remarks.** So far, this is the only *Endothyrella* species with two well-developed lamellae. The parietal lamellae show a very unusual arrangement which has not been ob-



**Figure 12.** Shells of *Endothyrella* and *Chersaecia* species. **A** *Endothyrella fultoni* (Godwin-Austen, 1892), NHMUK 1903.7.1.301. (syntype) **B** *Endothyrella aborensis* (Gude, 1915), (syntype, photos published in Gude 1915) **C** *Endothyrella miriensis* (Gude, 1915), NHMUK 1903.7.1.3205. (syntype). Photos **A** and **C** by H. Taylor. Scale represent 5 mm.

served in any other species of Plectopylidae. The two parietal plicae can be the result of teratological duplication which has been reported for some species (Gude 1908b: 347).

***Endothyrella affinis* (Gude, 1897)**

Figure 13G

1897b *Plectopylis affinis* Gude: Science Gossip, 3: 276, figs 41a–d. [“Khasia Hills, Assam”].  
1897g *Plectopylis affinis*, — Gude: The Journal of Malacology, 6: 46–48, fig. 3.

- 1899c *Plectopylis (Endothyra) affinis*, — Gude: Science Gossip, 6: 148.  
 1899d *Plectopylis (Endothyra) affinis*, — Gude: Science Gossip, 6: 175, 176.  
 1914b *Plectopylis (Endothyra) affinis*, — Gude: The Fauna of British India...: 73, 84–85, figs 34a–d.

**Types.** India, Khasia Hills, ex Fulton, NHMUK 1922.8.29.36 (syntype, Figure 13G); Khasia Hills, NHMUK 1901.4.25.41–43 (3 syntypes).

**Additional material examined.** India, Khasi Hills, NHMUK 1892.9.22.1–4 (4 specimens); India, NHMUK 1916.3.15.1–2/2 (“showing immature armature”); Khasi Hills, Assam, coll. Salisbury ex coll. Beddome, NHMUK 20150130/3; Khasi Hills, NHMUK 20150131/3; Cherra, leg. Godwin-Austen, NHMUK 20150132/1 juvenile shell; N-Vorderindien, Khasi-Berge, coll. C. R. Boettger 1911, SMF 118096/1 (labelled as “cotype”); Cherrapoonjee, coll. Jetschin ex coll. Gude 1900, SMF 118095/2; India, Khasi Hills, NHMW 34233/2; Khasi Hills, coll. Möllendorff, SMF 150107/3; Khasi-Berge, coll. Möllendorff, ex coll. Gude, SMF 9279/4; Khasi Hills, coll. Bosch ex coll. Rolle, SMF 172074/2; N. O(?) Indien, coll. Steenberg, ZMUC-GAS-1811/1; no locality, coll. Jousseume, MNHN 2012-27051/2; no locality, coll. Jousseume, MNHN 2012-27048/29 (strongly shouldered, relatively small shells together with typical ones).

**Diagnosis.** Shell small, sinistral, yellowish, with narrow umbilicus, conical dorsal surface and shouldered body whorl; hairs are arranged in four rows on the body whorl; callus strong, middle palatal plicae usually divided in the middle; the posterior fragments are oblique, the anterior ones are rather straight; parietal wall with a single, slightly curved lamella with short denticles posteriorly, one above and one below, and a horizontal lower plica which may be divided in the middle.

**Measurements** (in mm): D: 9.7–10.9, H: 5.4–5.7 (n = 4, SMF 9279); D: 8.5–10.6, H: 5.1–5.6 (n = 3, MNHN 2012-27048).

**Differential diagnosis.** See under *E. plectostoma*, *E. sowerbyi* and *E. tricarinata* and Table 5.

**Distribution.** The species is recorded from the Khasi Hills only (Figure 11).

***Endothyrella angulata* Budha & Páll-Gergely, sp. n.**

<http://zoobank.org/0359FD0B-BACA-4B47-A483-1DF6AD3F79A5>

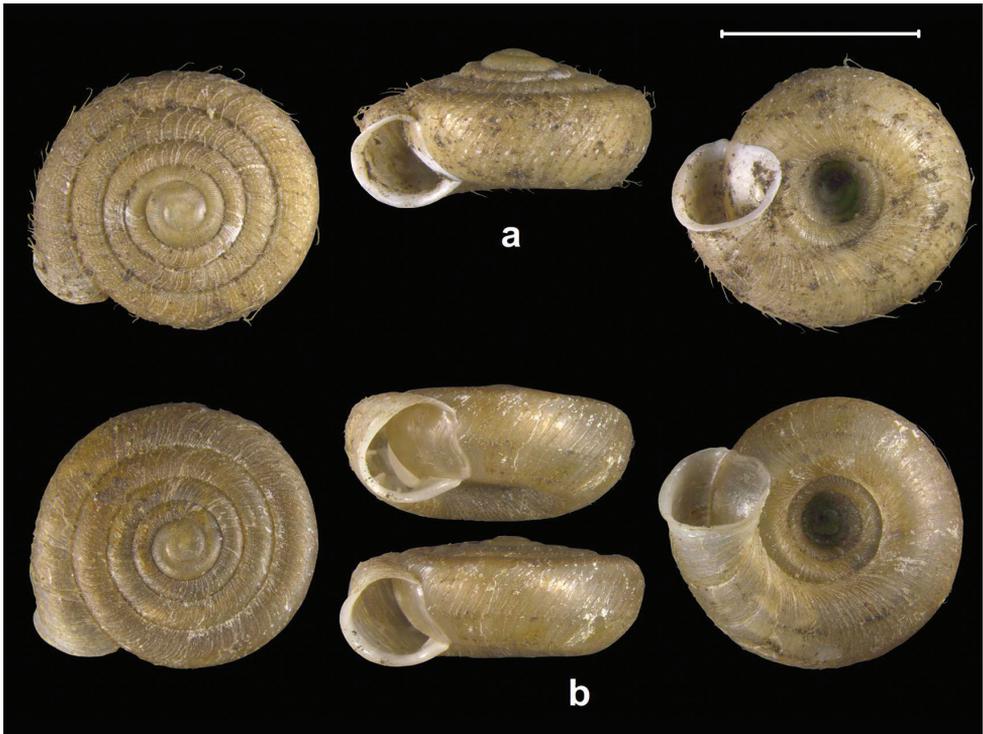
Figures 9I–J, 14B

**Type material.** Nepal, Taubas, Bhainse, Makwanpur District, 27°49'25.21"N, 85°04'48.39"E., leg. Budha, P., 30.03.2012., holotype (CDZMTU018, Figure 14B); 3 paratypes and 2 juvenile shells (not paratypes) (CDZMTU019).

**Diagnosis.** Shell small, sinistral, with flat dorsal surface and shouldered (keeled) body whorl; hairs are arranged in four rows; parietal lamella simple with a short free horizontal plica below it, and two denticles posterior to the lamella which are in contact with the lamella; middle palatal plicae divided.



**Figure 13.** Shells of *Endothyrella* species. **A** *Endothyrella plectostoma* (Benson, 1836), UMZC 102155 (syntype, specimen figured by Gude 1897b) **B** *Endothyrella plectostoma*, SMF 118091 **C** *Endothyrella sowerbyi* (Gude, 1899), NHMUK 1922.8.29.48. (holotype) **D** *Endothyrella sowerbyi*, SMF 346408 **E** *Endothyrella tricarinata* (Gude, 1897), UMZC 102170 (syntype of *tricarinata*) **F** *Endothyrella tricarinata*, NHMUK 1922.8.29.50. (syntype of *exerta*) **G** *Endothyrella affinis* (Gude, 1897), NHMUK 1922.8.29.26 (syntype). Photos: J. Gundry (**A, E**), B. Páll-Gergely (**B, D**) and H. Taylor (**C, F, G**). Scale represent 5 mm.

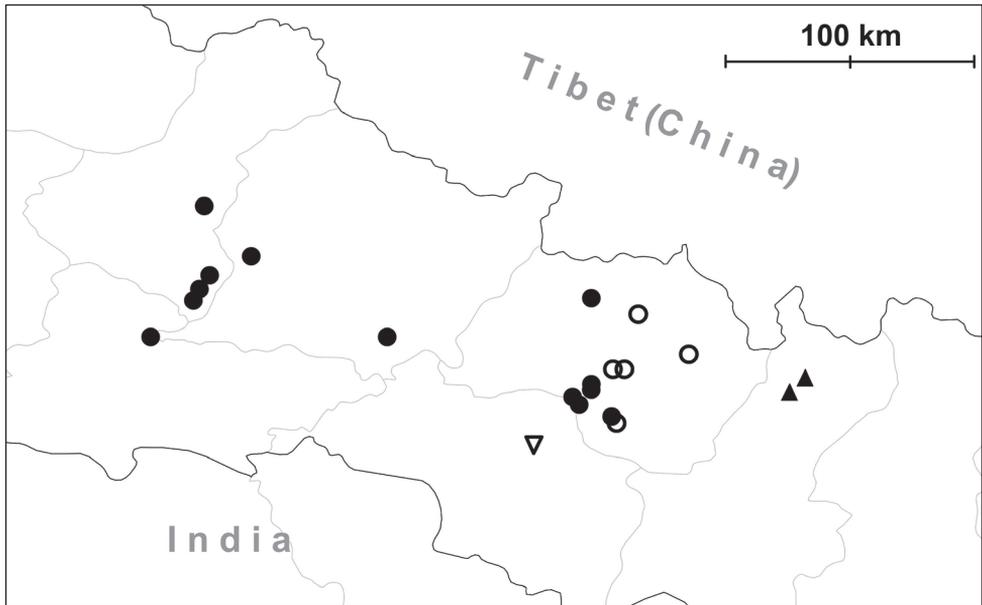


**Figure 14.** Shells of *Endothyrella* species. **A** *Endothyrella dolakhaensis* Budha & Páll-Gergely, sp. n., CDZMTU001 (holotype) **B** *Endothyrella angulata* Budha & Páll-Gergely, sp. n., CDZMTU018 (holotype). Both photos by E. Bochud. Scale represent 5 mm.

**Description.** Shell sinistral, semi-transparent; protoconch elevated from the flat dorsal surface; colour brownish or greyish; protoconch conspicuously large, consists of 2.5, 2.75 whorls, very finely, regularly ribbed; teleoconch with clearly visible reticulated sculpture dominated by radial growth lines; sculpture somewhat weaker on the ventral surface; very slender, long periostracal folds (hairs) standing in four spiral lines along the body whorl; two closely adjacent rows running with the keel above, one row on the ventral side around the umbilicus, and one row approximately in the middle line of the body whorl; whorls 6.25 (holotype) moderately bulging, separated by relatively deep suture; umbilicus wide and deep; peristome thin, slightly reflexed; callus moderate; no fold in the aperture.

One specimen was opened. Palatal wall with a single, straight lamella, with two short denticles on the posterior side of the lamella, both are in contact with the lamella; a short, free horizontal plicca is visible under the lamella; palatal wall with six plicae, first straight, last slightly curved, the middle plicae are divided in the middle, the fragments are horizontal, oblique or Z-shaped (Figure 9I–J).

**Measurements** (in mm): D: 8.5, H: 3.5 (holotype); D: 5.5, H: 2.5, Wh: 5 (paratype; subadult specimen).



**Figure 15.** Distribution of *Endothyrella* species in Nepal. Filled circle: *Endothyrella nepalica* sp. n.; filled triangle, top up: *Endothyrella dolakhaensis* sp. n.; empty triangle, top down: *Endothyrella angulata* sp. n.; empty circle: *Endothyrella minor*.

**Differential diagnosis.** See under *Endothyrella dolakhaensis* sp. n., *E. minor*, *E. nepalica* sp. n., *E. pinacis* and Table 5.

**Etymology.** The Latin *angulatus* (cornered, angular) refers to the shouldered/angularated body whorl of the new species.

**Type locality.** Nepal, Taubas, Bhainse, Makwanpur District, 27°49'25.21"N, 85°04'48.39"E.

**Distribution.** *Endothyrella angulata* sp. n. is known only from the type locality (Figure 15).

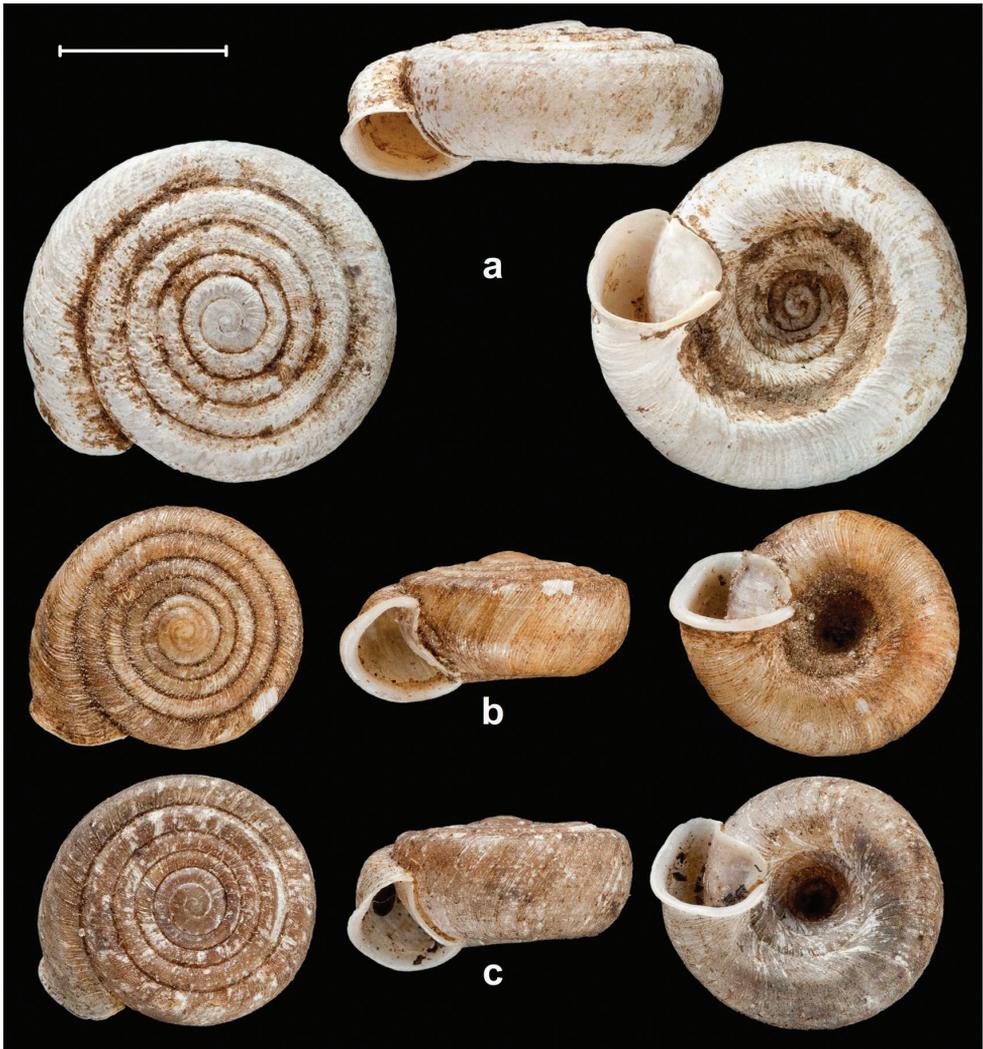
### *Endothyrella bedfordi* (Gude, 1915)

Figure 16C

1915 *Plectopylis* (*Chersaecia*) *bedfordi* Gude: Records of the Indian Museum, 8: 510–511, plate 42, fig. 2a–d. [“Abor country, Tsanspu Valley, on the Dihang, about 50 miles above the junction of the Sigon River, alt. 2800 ft.”].

**Types.** Tsanspu Valley Abor Hills, 2800 ft, leg. C.F.G. Oakes R.E., NHMUK 1903.7.1.3584. (2 syntypes, Figure 16C).

**Diagnosis.** Shell very small, sinistral, brownish, with moderately wide umbilicus, almost flat dorsal surface (only the apex is elevated slightly), and rounded body whorl; callus strong, palatal plicae long, more or less straight horizontal, with dichotomously



**Figure 16.** Shells of *Endothyrella* species. **A** *Endothyrella oakesi* (Gude, 1915), NHMUK 1903.7.1.3125. (syntype) **B** *Endothyrella brahma* (Godwin-Austen, 1879), NHMUK 1903.7.1.751. (syntype) **C** *Endothyrella bedfordi* (Gude, 1915), NHMUK 1903.7.1.3584. (syntype). All photos by H. Taylor. Scale represent 5 mm.

divided posterior ends and many small denticles at their posterior ends; lamella single, curved, in contact with a lower plica, which runs until the peristome.

**Measurements** (in mm): D: 9.1, H: 4.9 (n = 1, type series).

**Differential diagnosis.** *Endothyrella bedfordi* has a single curved parietal lamella with a long lower plica (which reaches the peristome) attached to it, and at the posterior ends of palatal plicae there are several small denticles. These features distinguish *E. bedfordi* from all congeners. See also Table 5.

**Distribution.** The species is known from the type locality only (approximately 28°44'N, 94°56'E) (Figure 10).

***Endothyrella blanda* (Gude, 1898)**

Figures 17B–C, 18, 19A–B, 20A–C

1898 *Plectopylis blanda* Gude: Science Gossip, 4: 264, figs 70 a–f. [“Naga Hills, Assam”]1899c *Plectopylis (Endothyra) blanda*, — Gude: Science Gossip, 6: 148.1899d *Plectopylis (Endothyra) blanda*, — Gude: Science Gossip, 6: 175, 176.1900 *Plectopylis blanda*, — Gude: The Journal of Malacology, 7: 34–35, figs 11a–f.1914b *Plectopylis (Endothyra) blanda*, — Gude: The Fauna of British India...: 73, 77–78, figs 28a–f.**Types.** Naga Hills, NHMUK 1922.8.29.41., coll. Godwin-Austen (holotype, Figure 17B).

**Additional material examined.** Richila Peak, Sikkim, India, coll. Ottó, L., MMGY 66425/2; Darjeeling, India, West Bengal, Darjeeling, North Point 900–1400 m asl., under stones in forest clearings, coll. Topál, 1967. HNHM 98849/2; Damsang, coll. Godwin-Austen, NHMUK 20150133/26; Rissetchu, Sikkim, coll. Godwin-Austen, NHMUK 20150135/8; Rissetchu & Richila Peak, W. Bhutan, coll. Godwin-Austen, NHMUK 20150136/33 (several of these are juvenile shells); Sikhim, Nampok, coll. Godwin-Austen, NHMUK 20150137/28; Richila Peak, Sikkim, coll. Godwin-Austen, NHMUK 20150138/102; Risset-Chu, Sikkim, NHMUK 20150139/309; Sikhim, NHMUK 20150140/8 (there is a label with the number “749”); Sikhim, coll. Beddome ex coll. Godwin-Austen, NHMUK 1912.4.16.318/1 (large variety); Sikhim, Rinkpo valley, NHMUK 1906.1.1.752/1; Sikkim, Rechila Peak, coll. W. Robert, NHMUK 1903.7.1.28/1; Sikhim, NHMUK 20150141/8; Sikkim, Rarhichu, coll. Godwin-Austen, NHMUK 20120110/1 (labelled as *hanleyi*?); Sikhim, Rarhichu, NHMUK 20150143/35 (mixed sample with *E. minor*); Darjiling, NHMUK 1906.2.2.142/5 (mixed sample with *E. plectostoma*); Rarhichu, NHMUK 20150134/49; Khasi Hills, leg. Stoliczka, 1880, NHMW 109255/3 (mixed sample with *E. plectostoma*: NHMW 92593 and *E. sowerbyi*: NHMW 109254).

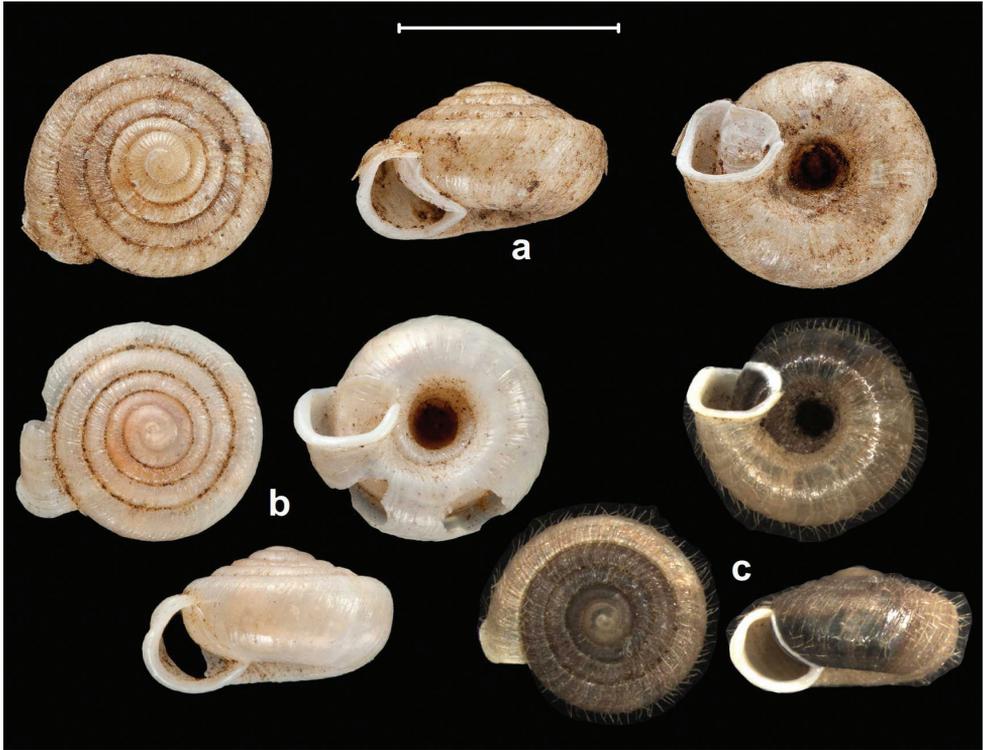
**Diagnosis.** Shell tiny to very small, sinistral, with narrow umbilicus, conical dorsal surface and 7 rows of hairs; callus weak but present; palatal plicae divided, posterior fractions denticle-like; anterior fractions horizontal, straight; lamella straight or very slightly S-shaped, with posterior denticles above and below, and with a lower and an upper plica close to the sutures; lower plica sometimes short, sometimes very long, and reaches the peristome.

**Measurements** (in mm): D: 4.9–5.7, H: 2.8–3.3 (n = 3, NHMUK 20150134).

**Differential diagnosis.** See under *E. macromphalus*, *E. minor*, *E. robustistriata* sp. n. and *E. williamsoni* and Table 5.

**Description of the genitalia** (Figure 18): Two specimens were anatomically examined. Collection data: Silchar Cachar, F. Ede, coll. Godwin-Austen, NHMUK 1903.7.1.502. Both specimens had several embryos developing in the uterus.

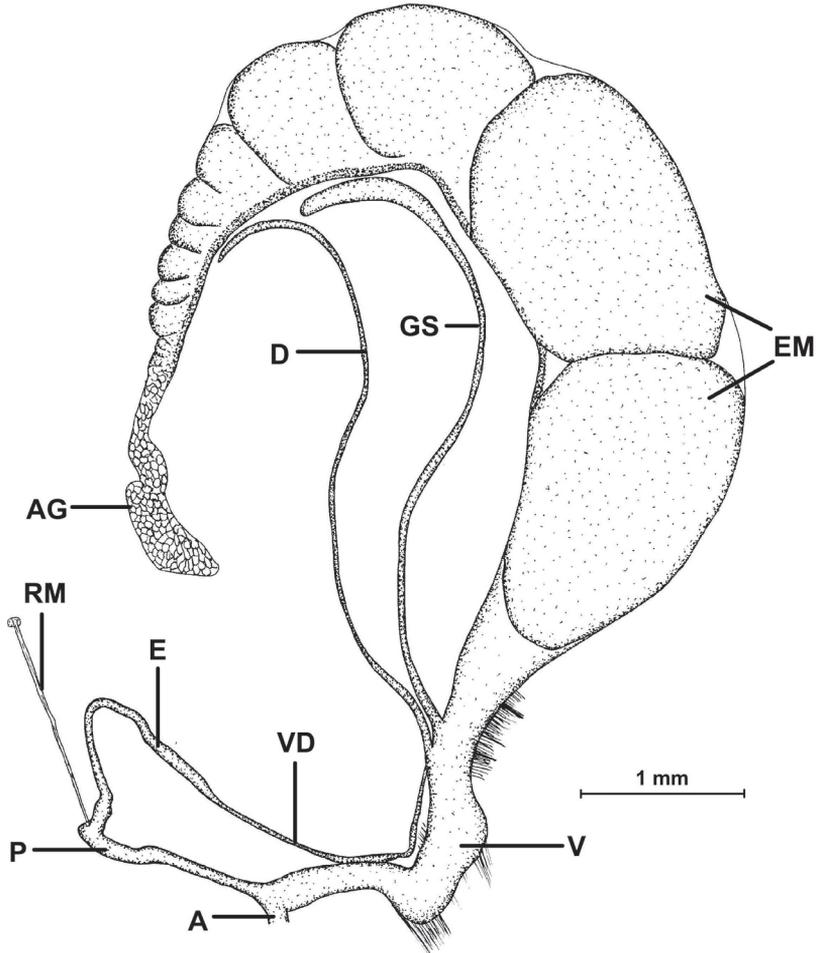
The left ommatophoral retractor passes between penis and vagina. Atrium short, penis long, rather cylindrical, but slowly tapers towards the proximal end; opening the penis was very difficult, not only because of its size, but also due to the age of the speci-



**Figure 17.** Shells of *Endothyrella* species. **A** *Endothyrella williamsoni* (Gude, 1915), NHMUK 1903.7.1.3087. (syntype) **B** *Endothyrella blanda* (Gude, 1898), NHMUK 1922.8.29.41. (holotype) **C** *Endothyrella blanda*, Silchar Cachar, F. Ede, coll. Godwin-Austen, NHMUK 1903.7.1.502. Photos: B. Páll-Gergely (**C**) and H. Taylor (**A, B**). Scale represent 5 mm.

men; the internal morphology could hardly be seen, although parallel folds forming “pockets” were visible; a little thickening was found near the posterior end of the penis, this could be interpreted as a penial caecum. The slender and relatively long retractor muscle inserts on the proximal end of the penis, slightly in proximal direction from the caecum; epiphallus also slender, slightly longer than the penis; vas deferens long and slim; vagina shorter than the penis and epiphallus combined, it is very thick, with a well-developed vaginal bulb; several short muscle fibres attach the vagina to the body wall and diaphragm; both the gametolytic sac and the diverticulum are very long and slim, although the gametolytic sac is somewhat thickened.

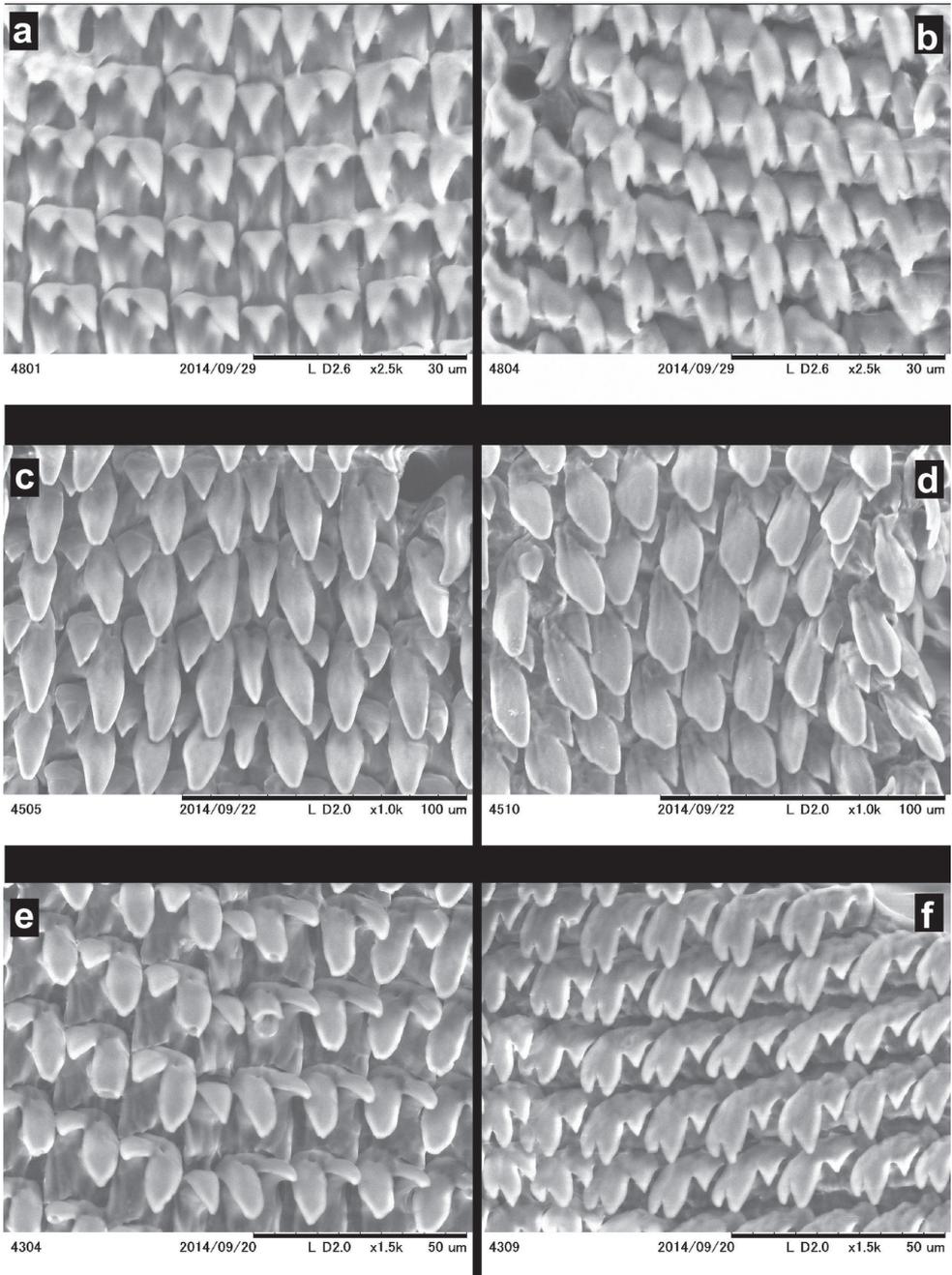
**Radula** (Figures 19A–B): Radula elongated, but not very slender, central tooth present, laterals approximately 6, standing in straight lines (perpendicular to the central column); marginals approximately 14, although it is difficult to distinguish which are laterals and which are marginals; marginals are placed in oblique rows; central tooth wide-based triangular, smaller than the endocone of the first lateral, but much larger than the ectocone; laterals bicuspid, endo- and ectocones are triangular; marginals usually tricuspid (the endocone has two cusps), but some of the marginals are



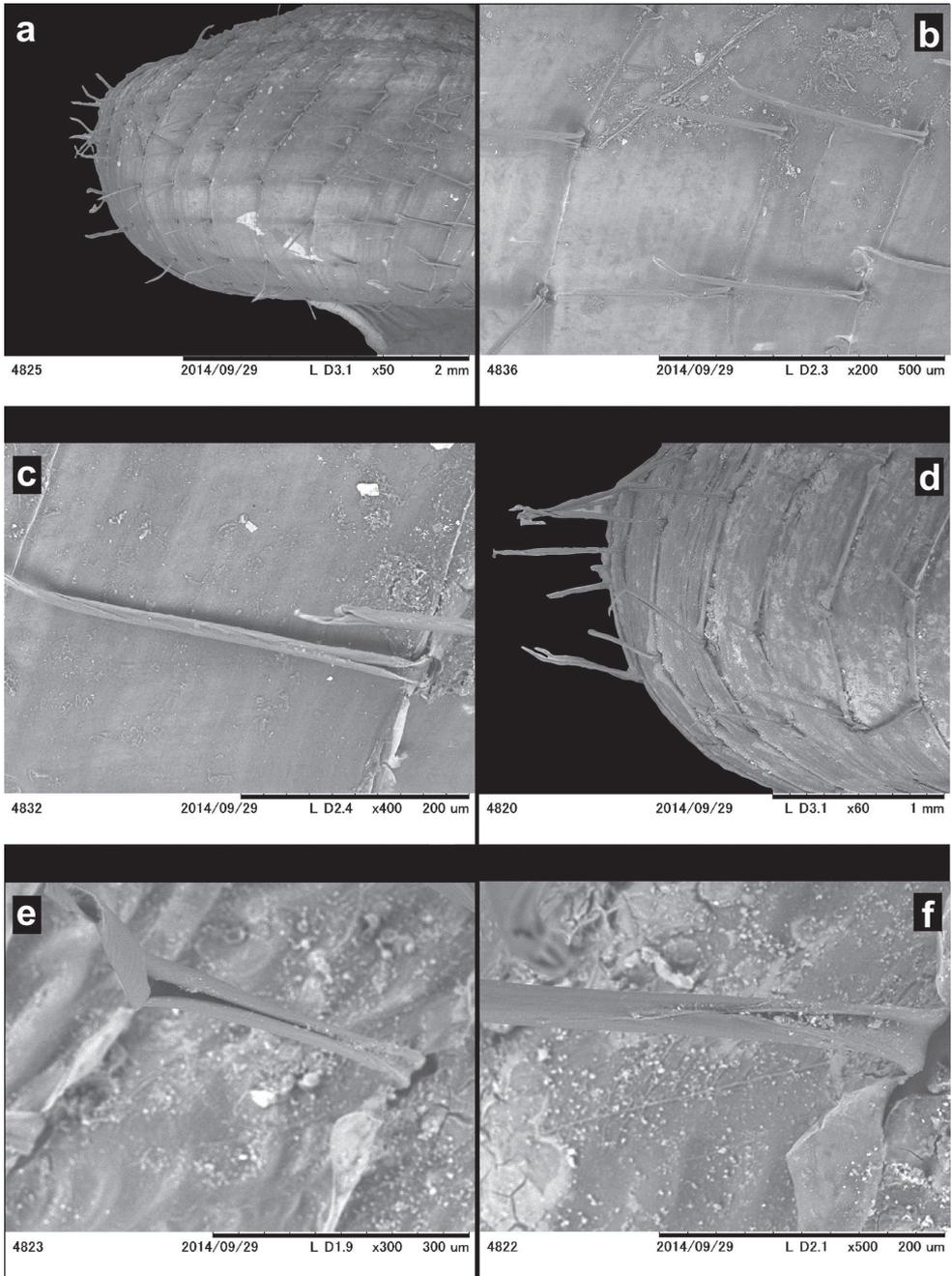
**Figure 18.** Genital anatomy of *Endothyrella blanda* (Gude, 1898). For locality see Fig. 17C. Abbreviations: **A** atrium **AG** albumen gland **D** diverticulum **E** epiphallus **EM** embryos **GS** gametolytic sac **P** penis **RM** retractor muscle **V** vagina **VD** vas deferens.

tetracuspoid (both the endocone and the ectocone have two cusps); all cusps pointed, the incision between the innermost two cusps is deep.

**Distribution.** Most museum samples have been collected in the Sikkim area. Gude received the holotype from Godwin-Austen, and it was said to be collected in the Naga Hills, approximately 600 km from Sikkim. The anatomically examined specimens have been collected from Silchar Cachar, which is located at least 500 km from Sikkim, but not far from the Naga Hills. If the samples from the Naga Hills and from Silchar are correctly labelled, we may expect that the species is widely distributed throughout north-eastern India (see also Figure 11).



**Figure 19.** SEM images of the radula of *Endothyrella* species. **A, C, E** central and adjacent lateral teeth **B, D, F** marginal teeth **A–B** *Endothyrella blanda* (Gude, 1898) (For locality see Fig. 17C) **C–D** *Endothyrella fultoni* (Godwin-Austen, 1892) (for locality see Fig. 18) **E–F** *Endothyrella plectostoma* (Benson, 1836), Sikhim, leg. Godwin-Austen, NHMUK 1903.7.1.451. All images by B. Páll-Gergely.



**Figure 20.** SEM images of *Endothyrella* shells. **A–C** *Endothyrella blanda* (Gude, 1898), For locality see Fig. 17C **D–F** *Endothyrella plectostoma* (Benson, 1836), Sikkim, leg. Godwin-Austen, NHMUK 1903.7.1.451. All images: B. Páll-Gergely.

***Endothyrella brahma* (Godwin-Austen, 1879)**

Figure 16B

- 1879a *Helix* (*Plectopylis*) *brahma* Godwin-Austen: Journal of the Asiatic Society of Bengal, 48 (2): 3–4, plate 1, fig 3. [“near Brahmakund, eastern Assam, at 1,000 feet elevation”].
- 1887 *Helix* (*Plectopylis*) *brahma*, — Tryon: Manual of Conchology..., 2 (3): 164, Plate 36, figs 35–37.
- 1894 *Plectopylis brahma*, — Pilsbry: Manual of Conchology, 2 (9): 145.
- 1897d *Plectopylis brahma*, — Gude: Science Gossip, 4: 170–171, figs 63a–c.
- 1899c *Plectopylis* (*Chersaecia*) *brahma*, — Gude: Science Gossip, 6: 148.
- 1899d *Plectopylis* (*Chersaecia*) *brahma*, — Gude: Science Gossip, 6: 175, 176.
- 1914b *Plectopylis* (*Chersaecia*) *brahma*, — Gude: The Fauna of British India...: 74, 113–114, 54a–c.
- 1915 *Plectopylis* (*Chersaecia*) *brahma*, — Gude: Records of the Indian Museum, 8: 509, 511.
- 1920 *Plectopylis* (*Chersaecia*) *brahma*, — Gude: Proceedings of the Malacological Society of London, 14 (2–3): 63.

**Types.** Brahmakund, E. Assam, NHMUK 1903.7.1.751. (6 syntypes, Figure 16B).

**Additional material examined.** Assam, leg. Hungerford, NHMUK 1891.3.17.362–364 (3 specimens); Assam, Brahmakund, coll. Godwin-Austen, NHMUK 20150144/27 (several shells juvenile); Brahmakund, NHMUK 20150145/8.

**Diagnosis.** Shell very small, sinistral, with narrow umbilicus, depressed conical dorsally, conspicuous radial sculpture without hairs; callus very strong; palatal plicae short, straight, with many small denticles at their posterior ends, standing along a vertical line; lamella oblique, with three horizontal plicae anteriorly, the lowermost is in contact with the lower end of the lamella; besides these anterior plicae, there is a short upper plica above the lamella, and long lower plica close to the lower suture, which runs until the aperture.

**Measurements** (in mm): D: 8.1–8.2, H: 4.6 (n = 2, type series).

**Differential diagnosis.** *Endothyrella brahma* can be distinguished from all other *Endothyrella* species by the presence of three parallel, horizontal parietal plicae anterior to the lamella. See also Table 5.

**Distribution.** The species is known from the type locality only (Figure 10).

***Endothyrella dolakhaensis* Budha & Páll-Gergely, sp. n.**

<http://zoobank.org/B1043A93-8B29-4E3E-A291-5AEED2E3B66F>

Figures 9G–H, 14A

**Type material.** Nepal, Suridobhan, Dolakha, 1023 m, 27.758852°N, 86.197894°E, leg. Budha, P., 03.02.2009., holotype (CDZMTU001, Figure 14A), CDZM-

TU002 (2 paratypes = shells from the same locality); Nepal, Bhorle, Dolakha, 800 m, 27.696652°N, 86.129583°E, leg. Budha, P., 03.02.2009., 11 paratypes = shells (CDZMTU003).

**Diagnosis.** Shell small with rather conical dorsal surface; body whorl slightly angulated with five rows of hairs; parietal lamella simple with one or two denticles posteriorly and a plica below; middle palatal plicae divided or almost divided.

**Description.** Shell very small, sinistral, with somewhat elevated spire and rather conical apex; protoconch elevated from the dorsal surface; colour brownish or greyish; protoconch conspicuously large, consists of 2.25–2.5 whorls ( $n = 2$ ), very finely, regularly ribbed; teleoconch with clearly visible reticulated sculpture dominated by radial growth lines; sculpture somewhat weaker on the ventral surface; very slender, long periostracal folds (hairs) standing in five spiral lines along the body whorl; whorls 5.25–5.5 ( $n = 3$ ) moderately bulging, separated by relatively deep suture; umbilicus wide and deep; apertural lip whitish, thin, slightly reflexed; callus also very weak, slightly S-shaped; no fold in the aperture.

One specimen from the type locality was opened. Parietal wall with one rather straight lamella with slight lower arms pointing in both directions; small denticle near the upper end posteriorly, connected to the lamella; two short horizontal plicae under the lamella; palatal wall with six plicae; first slim and short, the second–fifth plicae are divided in the middle and are of the same length; last plica also short, rather straight (Figures 9G–H).

**Measurements** (in mm): D: 6.5–9.0, H: 4.0–5.0., Wh: 5.5–6.0 ( $n = 5$ ).

**Differential diagnosis.** The most similar species are *E. affinis* and *E. plectostoma*, which are larger, have a higher spire, and a deeper, narrower umbilicus. *Endothyrella dolakhaensis* sp. n. has a more elevated spire and more rounded body whorl than *E. angulata* sp. n. Moreover, *E. dolakhaensis* sp. n. has five rows of periostracal folds, whereas *E. angulata* sp. n. has four. See also under *E. macromphalus*, *E. minor* and *E. nepalica* sp. n. and Table 5.

**Etymology.** The new species is named after the district name (Dolakha).

**Type locality.** Nepal, Suridobhan, Dolakha, 1023 m, 27.758852°N, 86.197894°E.

**Distribution.** *Endothyrella dolakhaensis* sp. n. is known from two localities in the valley of the Tamakoshi River, Dolakha district, Central Nepal (Figure 15).

### *Endothyrella fultoni* (Godwin-Austen, 1892)

Figures 12A, 19C–D, 21, 22B–C

1892 *Helix* (*Plectopylis*) *fultoni* Godwin-Austen: The Annals and Magazine of Natural History, 6 (10): 300–301. [“Exact locality unknown. Khasi Hills?”; detailed description on the exactness of the locality on page 301].

1893 *Plectopylis fultoni*, — Pilsbry: Manual of Conchology..., 2 (8): 296, 297.

1894 *Plectopylis fultoni*, — Pilsbry: Manual of Conchology..., 2 (9): 144, 146, Plate 40, figs 13–15.

- 1896 *Plectopylis fultoni*, — Gude: Science Gossip, 3: 178–179, figs 23a–b.  
1899c *Plectopylis (Endothyra) fultoni*, — Gude: Science Gossip, 6: 148.  
1899d *Plectopylis (Endothyra) fultoni*, — Gude: Science Gossip, 6: 175, 176.  
1914b *Plectopylis (Endothyra) fultoni*, — Gude: The Fauna of British India...: 72, 87–89, figs 36a–b.

**Types.** Khasi Hills (?) from Fulton, NHMUK 1903.7.1.301. (2 syntypes, Figure 12A).

**Additional material examined:** Ost-Ind., coll. Gerstenbrandt, NHMW 5954/2; Khasi Hills, Assam, coll. Rušnov, ex coll. Blume, NHMW 71770/R/9 (1 shell); Khasi Hills, leg. Godwin-Austen, NHMW 19599/2; India, Meghalaya, Khasi Hills, leg. Godwin-Austen, Altonaer Museum, ZMH 45907/2; Khasi-Berge, coll. Möllendorff, SMF 150103/3; Assam, Cherrapoonjeh, SMF 150104/4; Ostindien, Assam, coll. C. R. Boettger 1909, SMF 102818/1; Indien, Khasi Berge, coll. Bosch ex coll. Rolle, SMF 172070/3; Khasi Hills, coll. W. Blanford, NHMUK 1906.1.1.737/2; Khasi Hills, coll. Fulton, NHMUK 20150146/3; Assam, Khasi Hills, coll. Trechmann, NHMUK 20150147/2; Assam, Khasi Hills, NHMUK 1892.9.11.9–11/3 (one of them is small juvenile); Assam, Khasi Hills, coll. Lucas, NHMUK 20150148/2; Assam, Khasi Hills, coll. Smith, NHMUK 1937.12.30.13862–13864/3; India, Khasi Hills, coll. Salisbury ex coll. Beddome, NHMUK 20150149/2; Khasi Hills, Assam, coll. Gude, coll. Kennard, NHMUK 20150150/9; Assam, Cherrapoonje, coll. Lucas, NHMUK 20150151/1; no locality, dissected dried animal, NHMUK 20150152/3; no locality, coll. Jousseume, MNHN 2012-27052/1 juvenile shell.

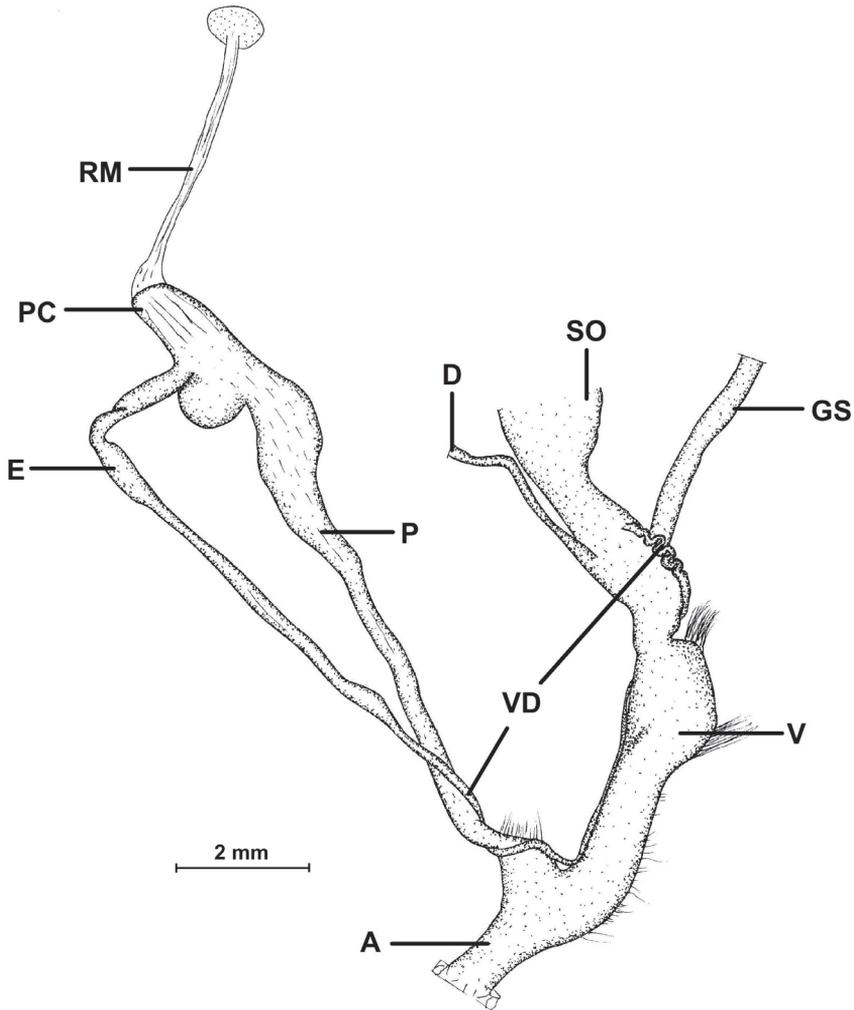
**Diagnosis.** Shell middle sized to large, sinistral, with reversed trapezoid shape, narrow umbilicus, angled body whorl, an apex which is elevated from the dorsal surface, and four rows of hairs on the body whorls; callus very strong; 3rd, 4th and 5th palatal plicae are divided in the middle, the others are more or less straight and horizontal; lamella vertical or oblique, with short lower and upper plicae above and below.

**Measurements** (in mm): D: 19.9–20.3, H: 9.5–10.4 (n = 2, SMF 150103).

**Differential diagnosis.** *Endothyrella fultoni* is much larger than any other *Endothyrella* species and has a characteristic reversed trapezoid shell shape. See also Table 5.

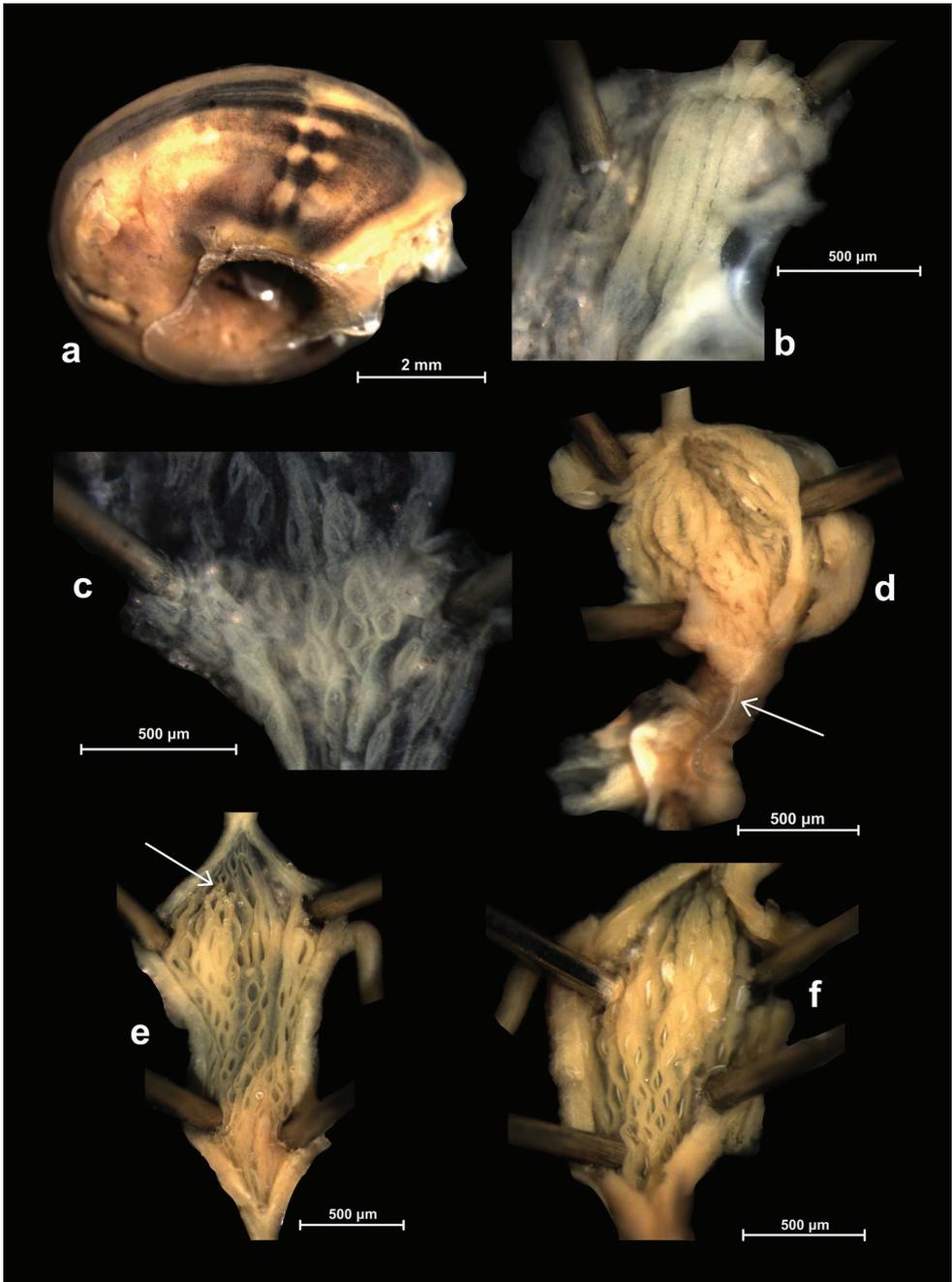
**Description of the genitalia** (Figures 21, 22B–C): A single specimen was anatomically examined. Collection data: Khasi, leg. Godwin-Austen, NHMUK 1903.7.1.598. The specimen had some embryos developing in the uterus. The whole body was very fragile, therefore the gametolytic sac and the diverticulum could not be dissected out.

The left ommatophoral retractor passes between penis and vagina. Atrium relatively long; penis long, consists of a longer, slimmer distal and a shorter, more thickened proximal part; at the proximal end of the penis there is a rounded bulb-like thickening (similar to that of some *Gudeodiscus* species, see Páll-Gergely and Asami 2014 and Páll-Gergely et al. 2015); penis internally with honey-comb-like tubercles without calcareous granules (Figure 22C); the somewhat slimmer penial caecum has some (approximately 8) parallel folds inside, which also form minute hollows standing in lines between the folds (Figure 22B); these small pockets may serve for small calcareous granules, although no granules were found; epiphallus enters penis at the basis of



**Figure 21.** Genital anatomy of *Endothyrella fultoni* (Godwin-Austen, 1892). Locality data: Khasi, leg. Godwin-Austen, NHMUK 1903.7.1.598. Abbreviations: **A** atrium **D** diverticulum **E** epiphallus **GS** gametolytic sac **P** penis **PC** penial caecum **RM** retractor muscle **SO** spermoviduct **V** vagina **VD** vas deferens.

the rounded penial thickening; epiphallus relatively short, approximately as long as the proximal, thickened part of the penis; retractor muscle inserts on the proximal end of the penial caecum, it is approximately as long as the proximal part of the penis; vas deferens long and thick, it becomes curly near its insertion to the spermoviduct; vagina shorter than the the half of the penis; it has a vaginal bulb at the middle; two batch of fibres attach the proximal and distal part of the vaginal bulb to the body wall; there are also some longer and more slender muscle fibres attached to the vagina; between the atrium and the vaginal bulb there is a slender, longitudinal thickening on the inner



**Figure 22.** Mantle pattern (**A**) and inner wall of the penis (**C–F**) and the penial caecum (**B**) of *Endothyrella* species. **A** *Endothyrella plectostoma* (Benson, 1836), For locality, see Fig. 19 **B–C** *Endothyrella fultoni* (Godwin-Austen, 1892), for locality see Fig. 21. **D–F** *Endothyrella plectostoma*, for locality, see Fig. 19. Arrow on **D** shows the entering point of the vas deferens to the penis. Arrow on **E** shows rounded calcareous granules. All photos by B. Páll-Gergely.

vaginal wall; vaginal bulb internally with fine, irregularly reticulated sculpture; the area of the inner vaginal wall between the bulb and the spermoviductus is roughly reticulated; gametolytic sac relatively thick, the diverticulum is more slender.

**Radula** (Figure 19C–D): The radula of the only available specimen was very fragile, probably because of the age of the sample; only a fragment of the middle part of the radula could be examined; central tooth present, laterals 14, marginals at least 8; central tooth very long, but somewhat shorter than the endocone of the first lateral, although larger than the ectocones; central tooth elongated triangular with slightly concave marginal line; endocone of the laterals are rather rhomboid, blunt, ectocone pointed triangular; endocones of marginals deformed rhomboid, sometimes oval, showing the sign of becoming bicuspid; ectocones of marginals blunt or pointed triangular.

**Distribution.** The species is assumed to occur in the Khasi hills (Godwin-Austen 1892) (Figure 11).

### ***Endothyrella macromphalus* (W. Blanford, 1870)**

Figures 23A–B

1870 *Helix* (*Plectopylis*) *macromphalus* W. Blanford: Journal of the Asiatic Society of Bengal, 39 (2): 17–18, Plate 3, fig. 14. [“ad Mairung in montibus Khasi”].

1870–1876 *Helix macromphalus*, — Hanley & Theobald: Conchologia Indica...: Plate 83, figs 8–10.

1875 *Plectopylis macromphalus*, — Godwin-Austen: Proceedings of the Zoological Society of London: 612, 613, Plate 73, figs 1, 1a. [“Darjeeling and N. E. frontier, Bengal. Khási”] (1874, part IV, published in 1875; see Duncan 1937).

1878 *Helix* (*Plectopylis*) *macromphalus*, — Nevill: Hand list of Mollusca in the Indian Museum, Calcutta...: 71.

1879b *Helix* (*Plectopylis*) *macromphalus*, — Godwin-Austen: The Annals and Magazine of Natural History, 5 (4): 163–164.

1887 *Helix* (*Plectopylis*) *macromphalus*, — Tryon: Manual of Conchology..., 2 (3): 160, Plate 34, figs 65–68.

1892 *Plectopylis macromphalus*, — Godwin-Austen: The Annals and Magazine of Natural History, 6 (10): 301.

1893 *Plectopylis macromphalus*, — Pilsbry: Manual of Conchology..., 2 (8): 297.

1894 *Plectopylis macromphalus*, — Pilsbry: Manual of Conchology..., 2 (9): 146.

1897c *Plectopylis macromphalus*, — Gude: Science Gossip, 4: 10–11, figs 46a–b. [“Khasia, Daffla and Naga Hills, in Assam”].

1899c *Plectopylis* (*Endothyra*) *macromphalus*, — Gude: Science Gossip, 6: 147, 148.

1899d *Plectopylis* (*Endothyra*) *macromphalus*, — Gude: Science Gossip, 6: 175, 177.

1914b *Plectopylis* (*Endothyra*) *macromphalus*, — Gude: The Fauna of British India...: 72, 79, figs 29a–b.

1915 *Plectopylis* (*Endothyra*) *macromphalus*, — Gude: Records of the Indian Museum, 8: 507.

1915 *Plectopylis (Endothyra) gregorsoni* Gude **new synonym**: Records of the Indian Museum, 8: 506–507, Plate 41, figs 2a–d. [“Yamne Valley, Abor Hills”].

**Types.** Darjiling, coll. W. Blanford, NHMUK 1906.1.1.754. (holotype of *macromphalus*, Figure 23A); Yamne Valley, Abor Hills, leg. C.F.G. Oakes, R.E., NHMUK 1903.7.1.3124. (holotype of *gregorsoni*, Figure 23B).

**Additional material examined.** Cherra, leg. Godwin-Austen, NHMUK 20150156/2 (juveniles, mixed sample with *E. affinis*); Khasi, leg. Stoliczka, 1880. xv.194., NHMW 92589/1 juvenile shell; Khasi Berge, SMF 150102/3 (mixed sample with *E. minor*); Khasi Berge, coll. Bosch, ex coll. Rolle, SMF 172069/2; Brit. Indien, Toruputu Dfola, 5000', coll. Ehrmann ex coll. Webb, SMF 150101/3; Daffa Hills, Burraill Gorge, coll. Godwin-Austen, NHMUK 1903.7.1.772/10 (4 had, 6 lacked a long lower plica); Khasi Hills, Mairang, coll. W. Blanford, NHMUK 1906.2.2.362/4 (3 lacked, 1 had a long lower plica); Khasi Hills, coll. Godwin-Austen, Figured in Godwin-Austen (1874), NHMUK 1903.7.1.766/9 (2 lacked, 7 had a long lower plica); Mairang, Khasi, NHMUK 1906.1.1.750/1; no locality, NHMUK 20150153/66 (19 shells had a long lower plica, 43 shells lacked, 4 corroded/dirty shells were not examined); Digny, coll. Godwin-Austen, NHMUK 20150154/1 (with long lower plica); Shillong, Khasi, “animal dissected”, NHMUK 1903.7.1.773/1 (with long lower plica); Teria Ghat, coll. Godwin-Austen, NHMUK 20150155/1 (with long lower plica); Toruputu Pk., Daffa Hills, NHMUK 1903.07.01.769/2 (mixed sample with *E. minor*); no locality, NHMUK 1871.9.23.68/4 (1 with, 3 without a long lower plica).

**Diagnosis.** Shell very small, sinistral with relatively wide umbilicus, reticulated, almost flat spire (only the apex is elevated) and smooth umbilical side; callus weak, only very slight whitish lime layer is visible; palatal plicae straight, divided or not, lamella with short upper and lower plicae and two posterior denticles, one above and one below; the lower plica might be long (see under Additional material examined).

**Measurements** (in mm): D: 5.5–8.2.2, H: 2.7–4.2 (n = 13, shells from different samples); the holotype of *Plectopylis gregorsoni* is 7.5 × 3.7 mm.

**Differential diagnosis.** *Endothyrella macromphalus* has more depressed shells than *E. blanda*. Moreover, *E. macromphalus* shells are smooth on the ventral side, whereas most *blanda* shells have hairs, or in case of corroded *E. blanda* specimens, holes which indicate the hairs' positions. *Endothyrella dolakhaensis* sp. n. is hairy, has weaker sculpture, and its spire is more elevated than in *E. macromphalus*. *Endothyrella robustistriata* sp. n. is smaller, has a narrower umbilicus and stronger dorsal sculpture. See also under *E. williamsoni* and Table 5.

**Distribution.** *Endothyrella macromphalus* seems to have a wide range including Assam and the Daffa and Khasi Hills. It has been reported from the Naga Hills, but those samples are probably misidentified. *Plectopylis gregorsoni* (treated here as a synonym of *E. macromphalus*) is recorded from the type locality only (approximately: 28°13.4'N, 95°13.3'E) (Figure 11).

**Remarks.** The type specimen of *Plectopylis gregorsoni* is very similar to typical *E. macromphalus* specimens. The main difference is that the palatal plicae are not divided



**Figure 23.** Shells of *Endothyrella* species. **A** *Endothyrella macromphalus* (W. Blanford, 1870), NHMUK 1906.1.1.754. (holotype of *macromphalus*) **B** *Endothyrella macromphalus*, NHMUK 1903.7.1.3124. (holotype of *gregorsoni*) **C** *Endothyrella robustistriata* sp. n., NHMUK 1903.7.1.767. **D** *Endothyrella robustistriata* sp. n., NHMUK 1903.7.1.3453. (holotype) **E** *Endothyrella minor* (Godwin-Austen, 1879), NHMUK 1891.3.17.358–359 (probably syntype) **F** *Endothyrella minor*, Nepal, Lalitpur, Phulchowki Hill, 2308 m, 27.574557°N, 85.400842°E, leg. Budha, P., 04.05.2007. Photos: B. Páll-Gergely (**C**) and H. Taylor (**A, B, D, E, F**). Scale represent 5 mm.

in *gregorsoni*, and the base is less glossy (rather weakly ribbed). In our view these minor difference are not sufficient for species level distinction, especially because *E. macromphalus* is a relatively variable species inhabiting wide geographical range. Very little is known about the distribution of specimens having divided or undivided palatal plicae. Therefore, until more information becomes available, *Plectopylis gregorsoni* is synonymised with *Endothyrella macromphalus*.

***Endothyrella minor* (Godwin-Austen, 1879)**

Figure 23E–F

1870 *Helix* (*Plectopylis*) *macromphalus* var. *minor*, — W. Blanford, Journal of the Asiatic Society of Bengal, 39 (2): 18. (no formal description presented) [“in valle Rungnu prope Darjiling in Sikkim”].

1879b *Helix* (*Plectopylis*) *minor* Godwin-Austen: The Annals and Magazine of Natural History, 5 (4): 164.

1895 *Helix* (*Plectopylis*) *minor*, — Godwin-Austen: Journal of the Asiatic Society of Bengal, 64: 154, Plate 7, figs 3, 3a.

1897c *Plectopylis minor*, — Gude: Science gossip, 4: 11, figs 47a–k.

1899c *Plectopylis* (*Endothyra*) *minor*, — Gude: Science Gossip, 6: 148.

1899d *Plectopylis* (*Endothyra*) *minor*, — Gude: Science Gossip, 6: 175, 177.

1914b *Plectopylis* (*Endothyra*) *minor* (partim), — Gude: The Fauna of British India...: 73, 75–77, figs 27a–l. [“Sikkim: Darjeeling”, “Rungun Valley”, “India: Naga Hills”, “Laisen Peak, Munipur” (this is the locality of *E. robustistriata* sp. n.)].

2015 *Endothyrella minor*, — Budha et al., ZooKeys, 492: 18–19.

**Types.** Darjiling, leg. Stoliczka, coll. Godwin-Austen, NHMUK 1903.07.01.768/10 syntypes. See also remarks.

**Additional material examined.** Nepal, Lalitpur, Phulchowki Hill, 2308 m, 27.574557°N, 85.400842°E, leg. Budha, P., 04.05.2007., 21 shells (Figure 23F); Nepal, Kathmandu, Chisapani, Shivapuri-Nagarjun National Park, 2361 m, 27.804855°N, 85.436468°E, leg. Budha, P., 11.06.2007., 5 shells; Nepal, Golphubhanjyan, Langtang National Park, Rasuwa, 3340 m, 27.873931°N, 85.757744°E, leg. Budha, P., 10.06.2007., 1 shell; Nepal, Shivapuri-Nagarjun National Park, Deurali, Baghdwar, 2386 m, 27.798318°N, 85.385448°E, leg. Budha, P., 25.04.2008., 1 shell; Nepal, Shivapuri-Nagarjun National Park, Shivapuri Peak, 2707 m, 27.810987°N, 85.383763°E, leg. Budha, P., 24.04.2008., 1 shell; India, Darjiling, leg. Stoliczka, coll. Oberwimmer, NHMW 71640/O/6881 (4 shells); Darjeeling, coll. Rolle, NHMW 71770/R/11 (3 shells); Darjiling, coll. Dr. Stoliczka, 1880, NHMW 91587/20; Darjeeling, coll. Möllendorff, SMF 150112/2; Darjeeling, coll. Webb, SMF 150111/2; Khasi Hills, NHMUK 20150159/3; Sikkim, Rarhichu, NHMUK 20150158/6 (mixed sample with *E. blanda*); India, Darjeeling, coll. Oldham, NHMUK 20150160/5; India, 1879.12.26.172–177/5; Sikkim, NHMUK 1906.2.2.361/3; Darjeeling, NHMUK 20150161/1 (there is a number “751”

on the bottom); Sikkim, NHMUK 1888.12.4.1525(?) (1 specimen); Darjeeling, under stones, 7000', coll. Everest Expedition 9 and 18.03.1924, NHMUK 20150162/5; Khasi Berge, SMF 345110/3 (ex *E. macromphalus*, SMF 150102); Toruputu Pk., Dafia Hills, NHMUK 1903.07.01.769/4 (mixed sample with *E. macromphalus*); Darjiling, coll. Hungerford ex coll. Nevill, NHMUK 1891.3.17.358–359 (Figure 23E).

**Diagnosis.** Shell tiny, sinistral, with relatively narrow umbilicus, flat dorsal surface and four rows of hairs; callus strong; palatal plicae divided; lamella straight or slightly curved, with two denticles posteriorly, one above and one below; lower plica can be short and in some specimens reaching the peristome.

**Measurements** (in mm): D: 4.9–5.3, H: 2.4–2.6 (n = 3, type series); D: 5–5.1, H: 2.4 (n = 3, SMF 345110); D: 4–5, H: 2–2.5, Wh: 5–5.5 (n = 12, Nepalese specimens).

**Differential diagnosis.** *Endothyrella minor* is smaller and has weaker keeled body whorl than *E. angulata* sp. n. Moreover, the first and second rows of the periostracal folds are comparatively at larger distance from each other in *E. minor* than in *E. angulata* sp. n. *Endothyrella blanda* has more elevated spire and more hair rows than *E. minor*. *Endothyrella robustistriata* sp. n. has more elevated spire than *E. minor* and lacks the hairs on its ventral surface. *Endothyrella macromphalus* is hairless and larger than *E. minor*, it has a comparatively larger protoconch and a lower (or missing) parietal callus. *Endothyrella minor* is smaller and flatter than *E. dolakhaensis* sp. n. Moreover, it has a more elevated parietal callus, and has only four rows of hairs (*E. dolakhaensis* sp. n. has five). See also under *E. williamsoni* and Table 5.

**Distribution.** Originally the species was recorded from Darjeeling, Sikkim area. Very similar specimens were found from Central Nepal in the surroundings of Kathmandu (Shivapuri-Nagarjun National Park and Phulchowki hill) and Langtang National Park. Some literature records (Laisen Peak, Naga Hills) are based on misidentified specimens (see Figure 11 and 15).

**Remarks.** W. Blanford (1870) described *Helix (Plectopylis) macromphalus*, and while giving information on its locality, he mentioned that “varietas minor” inhabits the Rungun valley near Darjeeling. No description or illustration of “varietas minor” was provided in the paper, therefore the name is not available. Later, Godwin-Austen (1879b) described *Helix (Plectopylis) minor* from “Darjiling hills” and mentioned those shell “no doubt are referable to *P. macromphalus* W. Blf., var. *minor*”. Blanford’s specimens labelled as *macromphalus minor* have not been found in the collection of the NHM, but the type sample examined and described by Godwin-Austen (NHMUK 1903.07.01.768) was found.

Recent fieldwork in Nepal yielded a few populations in the surroundings of Kathmandu which can be assigned to *E. minor*. “Typical” specimens of *E. minor* and Nepalese shells are very similar in terms of size, shell and aperture shape and the morphology of the plicae and lamellae. The only notable difference between these shells is the position of the hair rows on the body whorl. The first row is situated more upper in position (on the upper angle of the body whorl) in the Nepalese shells, whereas in typical shells the first row runs under the angle. Additionally, the distance between the third and fourth rows is smaller in the Nepalese populations.

***Endothyrella miriensis* (Gude, 1915)**

Figure 12C

1915 *Plectopylis* (*Endothyra*) *miriensis* Gude: Records of the Indian Museum, 8: 507–508, Plate 41, figs 3a–d. [“Miri Hills, Upper Assam”].

**Types.** Miri Hills, leg. C.F.G. Oakes, R.E., NHMUK 1903.7.1.3205. (4 syntypes, Figure 12C)

**Diagnosis.** Shell small, sinistral, with very slightly elevated spire, relatively wide umbilicus, and conspicuous spiral sculpture; callus moderately strong, palatal plicae slightly oblique, connected by a vertical ridge; lamella almost straight, with anteriorly elongated upper and lower ends and small denticles on the posterior side, one above and one below.

**Measurements** (in mm): D: 12.1–12.3, H: 5.3–5.4 (n = 2, type series).

**Differential diagnosis.** The unique spiral sculpture, which is very prominent on the ventral side as well, distinguishes *E. miriensis* from all congeners. See also Table 5.

**Distribution.** The species is known from the type locality only (Figure 10).

***Endothyrella nepalica* Budha & Páll-Gergely, sp. n.**

<http://zoobank.org/1ED614EA-455F-4507-B1EF-F5129052F4E0>

Figures 6E, 8A–C, 9C–F, 24A–C, 25

2015 *Endothyrella affinis*, — Budha et al., ZooKeys, 492: 18.

**Type material.** Champadevi, Kirtipur, Kathmandu District, 1326–1500 m, 27.654868°N, 85.244084°E, leg. Budha, P., 02.10.2010., holotype (CDZMTU005.1), paratypes CDZMTU005.2–16 (15 shells), CDZMTU005P (2 paratypes = specimens dissected and preserved, 3 dry shells = paratypes, 2 juvenile shells = not paratype); W-Nepal, Dhaulagiri Zone, Myagdi District, Annapurna Conservation Area, right side of Kali Gandaki valley, 300 m NNW of Suke Bagar village along “Tatopani-Dana” track, 1430 m alt., 14.05.1996., leg. A. Kuznetsov, WM/10 paratypes; Nepal, Kathmandu Valley, NW end of Kathmandu, middle part of S slope of Swoyambhunath Hill, in dry oak forest, 1500 m, 25.04.1995, leg. A. Kuznetsov, WM/4 sinistral and 1 dextral paratypes; W Nepal, Daulagiri zone, Hyagdi distr., Annapurna NP., right side of Kali Gandaki v., NNW of Suke Bagar, Tatop, leg. A. Kuznetsov, 14.05.1996., ex coll. W. Maassen, HNHM 95867/1 paratype (labelled as paratype of “*Plectopylis nepalensis* Schileyko and Kuznetsov”); Nepal, Swoyambhunath, Kathmandu District, 1366 m, 27.716971N, 85.289386 E, leg. Budha, P., 05.09.2008, CDZMTU006 (24 paratypes = shells); Siddha Cave, Tanahun District, 600 m, 27.94718°N, 84.421338°E, leg. Budha, P., 24.10.2008, CDZMTU004, CDZMTU007 (11 paratypes = shells, and one juvenile shell, which is not paratype) (Figs 6E, 24A); Dhunche, Rasuwa, 1985 m, 28.1092°N, 85.2916°E, leg. Budha, P., 31.05.2007., CDZMTU008 (2 shell = paratypes, and one damaged shell which is not paratype); Balaju,

Kathmandu District, 1356 m, 27.741173°N, 85.293763°E, leg. Budha, P., 04.01.2009., CDZMTU009 (8 paratypes = shells), CDZMTU009P (2 paratypes = specimens preserved, 4 dry shells = paratypes); Mahadevsthan, Thankot, Kathmandu District 1500 m, 27.683366°N, 85.213834°E, leg. Budha, P., 06.02.2007., CDZMTU010 (25 paratypes = shells), CDZMTU010P 2 paratypes = specimens preserved, 4 dry shells = paratype, 5 juvenile shells = not paratypes); Arjewa, Baglung, 900 m, 28.154393°N, 83.630703°E, leg. Budha, P., 13.09.2006., CDZMTU011 (14 paratypes = shells, one juvenile shells = not paratype); Majhbeni, Parbat, 700 m, 28.205708°N, 83.674605°E, leg. Budha, P., 13.09.2006., CDZMTU012 (9 paratypes = shells, 6 juvenile/damaged shells = not paratypes); Sirsuwa, Parbat District, 780 m, 28.136478°N, 83.642135°E, leg. Budha, P., 13.09.2006., CDZMTU013 (6 paratypes = shells); Foksing, Parbat District, 790 m, 28.093252°N, 83.604283°E, leg. Budha, P., 11.06.2006., CDZMTU014 (11 paratypes = shells, 2 juvenile shells 7 not paratypes); Godawari, Lalitpur, 1868 m, 27.94718°N, 84.421338°E, leg. Budha, P., 01.10.2008., CDZMTU015a (1 paratype); Annapurna Conservation Area, Tatopani, 1282 m, 28.495172°N, 83.628883°E, leg. Budha, P., 01.10.2008., CDZMTU016 2 (2 paratypes = shells); Godawari, Lalitpur, 1575 m, 27.596459°N, 85.389432°E, leg. Budha, P., 30.06.2007., CDZMTU015b (1 paratype = shell); Ridi, Gulmi, 832 m, 27.945621°N, 83.43215°E, leg. Budha, P., 30.06.2007., CDZMTU017 (5 paratypes = shells); Godawari Botanical Garden, Lalitpur, 1453 m, 27.596671°N, 85.381758°E, leg. Budha, P., 03.09.2008., CDZMTU015c (50 paratypes = shells); Nepal, Pokhara, Khare, 1520 m alt., 28.2860°N, 83.8472°E, leg. C. Huber, 18.03.1991, NMBE 527538/1 paratype (Figure 24C).

**Diagnosis.** A small to middle-sized, hairless species with domed dorsal surface and rounded body whorl; parietal lamella simple with one or two denticles posteriorly and sometimes a plica below the lamella, middle palatal plicae divided or almost divided.

**Description.** Shell very small to small, sinistral, with somewhat elevated spire and domed dorsal surface; protoconch slightly elevates from the dorsal surface; usually brownish but sometimes turns into yellowish; protoconch consists of 1.5–1.75 whorls, very finely, regularly ribbed; teleoconch with very weak, irregular growth lines on the ventral surface and fine reticulated sculpture on the dorsal surface; in high magnification the surface is covered by flat periostracal folds; no spirally arranged large deciduous folds found; whorls 5.5–6.25, moderately bulging, separated by relatively deep suture; umbilicus wide and deep, whorls almost flat inside, resulting in an funnel-like shape, apertural lip whitish, rather thin, slightly reflexed; callus inconspicuous, but present, slightly S-shaped; no fold in the aperture.

Ten specimens were opened from different populations. Parietal wall with one slightly curved lamella with arms pointing in the direction of the aperture; lower end on the lamella more conspicuously curved than the upper end; two small denticles above and below posteriorly of the lamella (exceptionally, the lower one is missing); in some populations (e.g. Majhbeni – Parbat District, Champadevi – Kathmandu District and Siddha Cave – Tanahu District) with short plica under the lamella; palatal wall with six plicae; first slim and short, parallel with the suture; second plica is the longest, it shows a tendency towards dividing in the middle, but the two parts always fused;

third, fourth and fifth plicae usually divided (third one sometimes not); last plica short, slightly curved with arms pointing in the direction of the lower suture (Figures 9C–F).

**Measurements** (in mm): D: 8.2–14.9, H: 4.0–6.0, Wh: 5.5–7.5 (n = 35, different populations).

**Differential diagnosis.** *Endothyrella nepalica* sp. n. is usually larger than *E. angulata* sp. n., it has a domed dorsal surface, rounded body whorl and lacks hairs standing in spiral rows, whereas *E. angulata* sp. n. has a flat dorsal surface, shouldered body whorl and has hairs which are arranged in spiral rows. *Endothyrella dolakhaensis* sp. n. differs from *E. nepalica* sp. n. by the usually smaller size, fewer whorls, stronger sculpture, comparatively larger protoconch, conical dorsal surface, slightly angulated body whorl and the presence of hairs standing in five spiral lines. For comparison with *E. oakesi* and *E. pinacis*, see under those species. See also Table 5.

**Description of the genitalia** (Figures 25A–C): Three specimens from three populations were anatomically examined (Champadevi, Balaju of Kathmandu District and Godawari Botanical Garden, Lalitpur District). Penis short, narrow distally and slowly tapers toward the proximal end; internal surface with several tubercles including minute calcareous hooks; epiphallus slender, cylindrical, longer than the penis, it enters penis laterally; penial caecum very short, blunt, cylindrical, with a short retractor muscle attached at its proximal end; vas deferens thin and nearly 1.5 times longer than epiphallus, convoluted before connection to prostate; vagina shorter than the penis with well-developed vaginal bulb; gametolytic sac very thin throughout and ends into a small rounded sac; there is a slender diverticulum running parallel with the gametolytic sac; it is as long as the gametolytic sac.

**Etymology.** The name *nepalica* refers to the country (Nepal) where the new species lives.

**Type locality.** Champadevi, Kirtipur, Kathmandu District, Nepal, 1326–1500 m, 27.654868°N, 85.244084°E.

**Distribution.** *Endothyrella nepalica* sp. n. inhabits a relatively large area in western and central Nepal (Figure 15).

**Remarks.** Schileyko (1999) figured a shell from the “SW slope of Swayambhunat (= Swoyambhunath) hill, Kathmandu valley, Nepal” (Fig. 594.). The figured specimen is probably *Endothyrella nepalica* sp. n., but the drawing is not sufficient for identification.

### ***Endothyrella oakesi* (Gude, 1915)**

Figure 16A

1915 *Plectopylis* (*Endothyra*) *oakesi* Gude: Records of the Indian Museum, 8: 505–506, Plate 41, Figs 1a–d. [“Yamne Valley, Abor Hills and Sibbum”, “between Riu and Singging, on the Dihang River”].

**Types.** Yamne Valley, Abor Hills, leg. C.F.G. Oakes, R.E., NHMUK 1903.7.1.3125 (5 syntypes, Figure 16A).

**Additional material examined.** Sibbum, Abor, NHMUK, coll. Godwin-Austen, NHMUK 20150157/1; Abor Hills, “exact position not known”, below alt. 3000' between lat. 28°15'+29°15', long. 94°50'+95°10', leg. Oakes, coll. Godwin-Austen, NHMUK 1903.7.1.3125/1.

**Diagnosis.** Shell small, sinistral, with wide umbilicus, and slightly domed dorsal surface; callus strong, palatal plicae complicated, their anterior part is horizontal, but the posterior part vertical; there are several short horizontal plicae between posterior parts of the palatal plicae; lamella almost straight with posteriorly elongated upper end, and sometimes with a long lower plica which reaches the aperture.

**Measurements** (in mm): D: 11.7–12.5, H: 4.7–5.5 (n = 3, type series).

**Differential diagnosis.** *Endothyrella nepalica* sp. n. also has simpler palatal plicae than those of *E. oakesi*. Moreover, *E. nepalica* sp. n. has a flatter shell and a less descending aperture. See also under *E. pinacis* and Table 5.

**Distribution.** This species was reported only from the localities mentioned in the original description (Yamne Valley, Abor Hills and Sibbum), “between Riu and Singing, on the Dihang River” (Figure 10).

**Remarks.** Three specimens (two adults and a juvenile) of the type lot of *E. oakesi* were opened (probably by Gude). The long lower parietal plica, described as characteristic feature of this species, is present only in one specimen. In face of this, *Endothyrella oakesi* seems to be a distinct species on the basis of the palatal plicae and shell shape.

### *Endothyrella pinacis* (Benson, 1859)

Figures 24D–F

1859 *Helix pinacis* Benson: The Annals and Magazine of Natural History, 3 (3): 268–269. [“Habitat raro in regione Sikkim in valle Rungun (4000 ped.), necnon prope Pankabari (1000 ped. alt.)”].

1860 *Helix (Plectopylis) pinacis*, — Benson: The Annals and Magazine of Natural History, 3 (5): 243–247. [“Darjiling and the Khasia Hills”].

1868 *Helix pinacis*, — Pfeiffer: Monographia Heliceorum Viventium..., 5: 417.

1868 *Helix (Corilla) pettos* Martens: Malakozoologische Blätter, 15: 158.

1869 *Helix pettos*, — Pfeiffer: Novitates conchologicae...: 462–463.

1872 *Helix pinacis*, — Hanley & Theobald: Conchologia Indica...: 7, 36, Plate 13, fig. 5, Plate 84, figs 1–4. [“Sikkim (Rungun, and near Pankabari)”].

1875 *Plectopylis pettos*, — Godwin-Austen: Proceedings of the Zoological Society of London, 612. [“Himalaya?”].

1875 *Helix (Plectopylis) pinacis*, — Godwin-Austen: Proceedings of the Zoological Society of London: 612, 613, plate 74, fig. 1 (1874, part IV, published in 1875; see Duncan 1937).

1878 *Helix (Plectopylis) pinacis*, — Nevill: Hand list of Mollusca in the Indian Museum...: 71.

1879b *Helix (Plectopylis) pinacis*, — Godwin-Austen: The Annals and Magazine of Natural History, 5 (4): 163.

- 1887 *Helix* (*Atopa*) *pettos*, — Tryon: Manual of Conchology..., 2 (3): 156, Plate 34, figs 36–38.
- 1887 *Helix* (*Plectopylis*) *pinacis*, — Tryon: Manual of Conchology...2 (3) 159–160, Plate 34, figs 53–55.
- 1894 *Plectopylis pinacis*, — Pilsbry: Manual of Conchology..., 2 (9): 144, 146.
- 1894 *Plectopylis pettos*, — Pilsbry: Manual of Conchology..., 2 (9): 146.
- 1895 *Plectopylis pinacis*, — Godwin-Austen: Journal of the Asiatic Society of Bengal, 64: 154, Plate 7, figs 2, 2a.
- 1897a *Plectopylis pinacis*, — Gude: Science Gossip, 3: 206, figs 32a–d.
- 1897a *Helix* (*Corilla*) *pettos* = *Plectopylis pinacis*, — Gude: Science Gossip, 3: 206.
- 1899c *Plectopylis* (*Endothyra*) *pinacis*, — Gude: Science Gossip, 6: 147, 148.
- 1899c *Plectopylis* (*Endothyra*) *pettos* (under *pinacis*), — Gude: Science Gossip, 6: 148.
- 1899d *Plectopylis* (*Endothyra*) *pinacis*, — Gude: Science Gossip, 6: 175, 177.
- 1899d *pettos*, — Gude: Science Gossip, 6: 177.
- 1907 *Plectopylis pinacis*, — Godwin-Austen: Land and freshwater Mollusca of India...: 203–204.
- 1914b *Plectopylis* (*Endothyra*) *pinacis*, — Gude: The Fauna of British India..., 72, 86–87, figs 35a–d. [“Sikkim : Darjeeling”, “Rungun, Pankabari”, “Rungmaival”, “Damsang”].
- 1914b *Plectopylis* (*Endothyra*) *pinacis*, — Gude: The Fauna of British India...: 72, 86.
- 1915 *Plectopylis* (*Endothyra*) *pinacis*, — Gude: Records of the Indian Museum, 8: 506, 508.

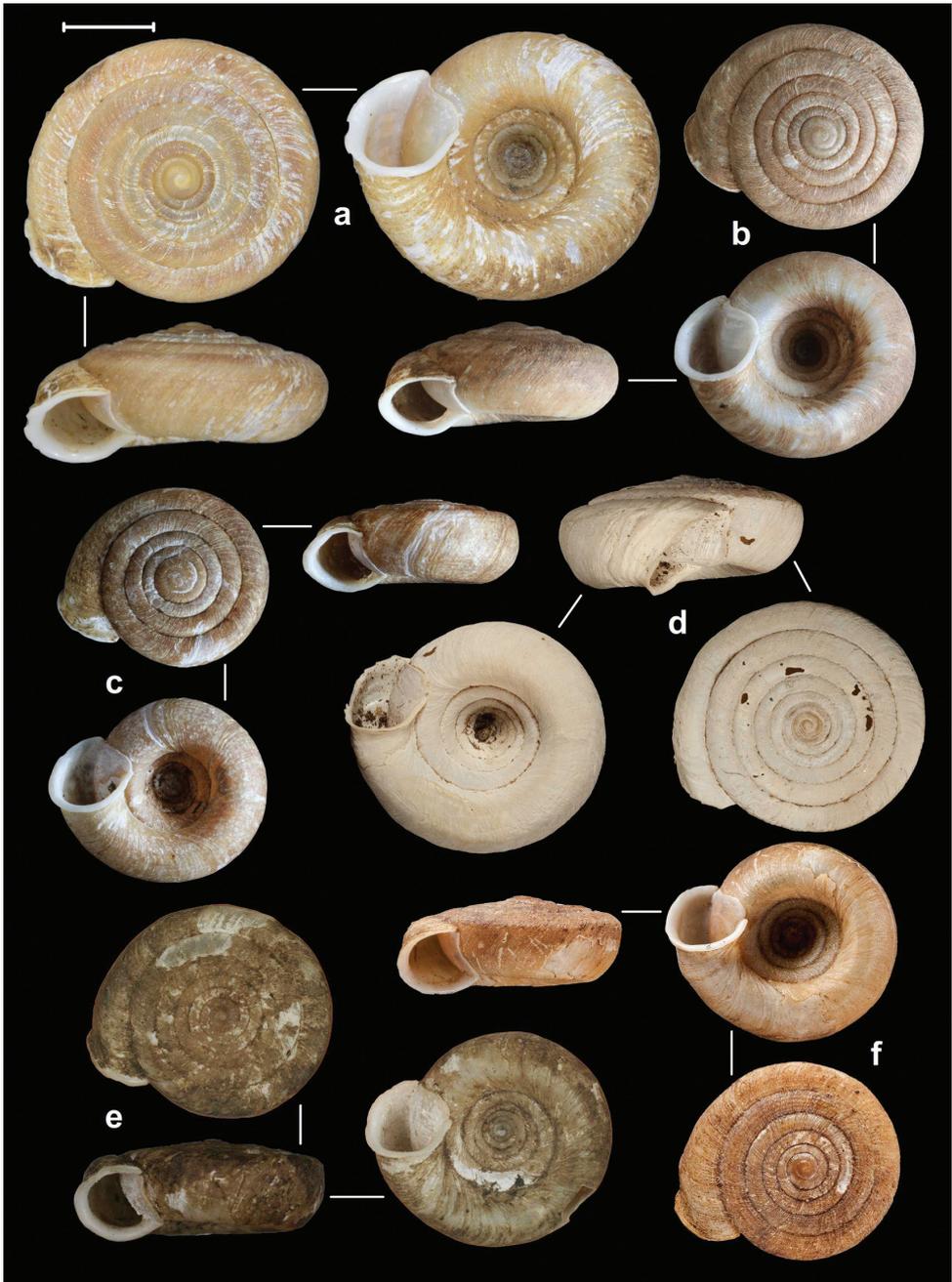
**Types.** Sikkim, coll. Benson, UMZC 102755 (holotype of *Helix pinacis*, Figure 24D); Himalaya, ZMB/MOLL 17905 (holotype of *Helix pettos*, Figure 24E).

**Additional material examined.** India, West Bengal, Darjeeling District, Lopchu + Ghum, coll. Topál, 21–22.04.1967, locality code: 869, HNHM 98848/2; Darjiling, coll. Dr. Stoliczka, 1880, NHMW 92590/7; Sikkim, coll. Möllendorff, SMF 150110/6 (3 of them juvenile); Darjeeling, coll. Bosch, ex coll. Rolle, SMF 172075/2; Darjiling, figured in Godwin-Austen (1874), coll. Godwin-Austen, NHMUK 1903.7.1.746/5; Darjiling, coll. W. Blanford, NHMUK 1860.6.27.14 (1 specimen); Kungna valy. (?) Sikkim., NHMUK 20150163/2; Darjiling, NHMUK 1906.2.2.143/2 (Figure 24F); Damsang Peak, Daling Hills, coll. Godwin-Austen, NHMUK 20150164/26 (several of the juvenile); Sikkim, Rarhichu, NHMUK 20150165/5; Rechila Peak, coll. Godwin-Austen, NHMUK 20150167/1; Darjiling, NHMUK 1888.12.4.1524/1; Darjeeling, 5000', coll. Everest Expedition 1924, NHMUK 20150168/1; Rarkichu, Sikkim, coll. Godwin-Austen, NHMUK 20150166/1.

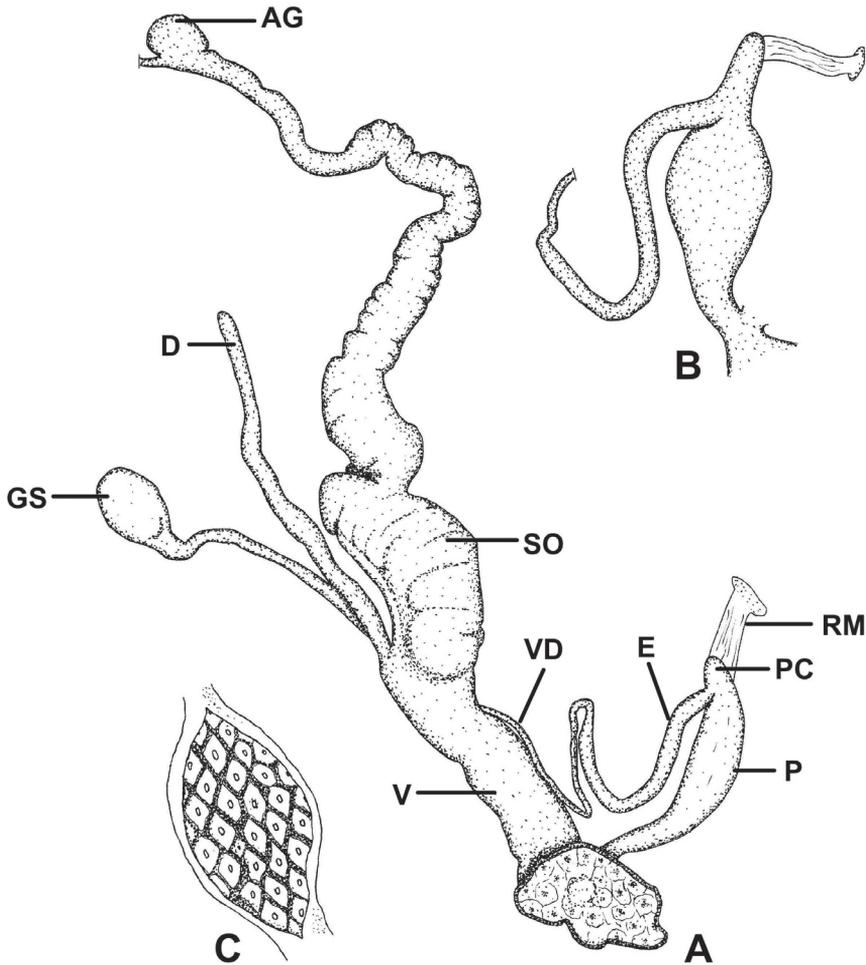
**Diagnosis.** Shell very small to small, sinistral, hairless, with wide umbilicus and slightly angulated body whorl; callus strong, palatal plicae short and oblique, lamella rather straight with anteriorly elongated upper and lower ends, and posteriorly elongated upper end; there are two denticles on the posterior side of the lamella, one above and one below, the lower one might be in contact with the lamella.

**Measurements** (in mm): D: 13.6–14.1, H: 5.9–6.1 (n = 3, SMF 150110).

**Differential diagnosis.** *Endothyrella angulata* sp. n. is usually smaller than *E. pinacis*, it has a stronger keel and has weaker spiral lines on the ventral side of the shell, which are



**Figure 24.** Shells of *Endothyrella* species. **A** *Endothyrella nepalica* Budha & Páll-Gergely, sp. n., paratype, same data as on Fig. 6E **B** *Endothyrella nepalica* Budha & Páll-Gergely, sp. n., holotype **C** *Endothyrella nepalica* Budha & Páll-Gergely, sp. n., paratype, NMBE 527538 **D** *Endothyrella pinacis* (Benson, 1859), (holotype of *pinacis*) **E** *Endothyrella pinacis* (holotype of *Helix pettos*) **F** *Endothyrella pinacis*, NHMUK 1906.2.2.143. Photos: B. Páll-Gergely (**A**), E. Bochud (**B, C**), J. Gundry (**D**), Ch. Zorn (**E**), H. Taylor (**F**). Scale represent 5 mm.



**Figure 25.** Genital anatomy of *Endothyrella nepalica* sp. n. **A** Specimen from Godawari **B, C** penis of a specimen from Balaju. Diagrammatic. Abbreviations: **AG** albumen gland **D** diverticulum **E** epiphallus **GS** gametolytic sac **P** penis **PC** penial caecum **RM** retractor muscle **SO** spermoviduct **V** vagina **VD** vas deferens.

clearly visible in *E. pinacis*. The most similar species is *Endothyrella nepalica* sp. n., which nevertheless has a higher spire and rounded whorls, whereas *E. pinacis* has shouldered whorls and nearly flat dorsal surface. The ventral surface of the two species is similar, but *E. pinacis* has slender hairs standing in 3 lines, which is missing in *E. nepalica* sp. n. According to previous studies (Godwin-Austen 1889–1914, Schileyko 1999) *E. pinacis* has no diverticulum, but in all *E. nepalica* sp. n. we dissected that organ was present. *Endothyrella oakesi* is similar to *E. pinacis*, but has much more complicated palatal plicae, more descending aperture, differently shaped umbilicus and rounded body whorl. See also Table 5.

**Anatomy.** The anatomy of *Endothyrella pinacis* was described by Godwin-Austen (1889–1914) and Schileyko (1999). According to these descriptions, only the gametolytic sac is present and the diverticulum is missing. The penial caecum seems to be missing, although none of these drawings show this part clearly. Other features of the genitalia (penis shape, internal wall of the penis, vagina) are similar to those of *E. nepalica* sp. n.

**Radula.** Stoliczka (1871) mentioned that the central tooth is larger than that of *Plectopylis achatina* (= *bensoni*), and that its shape is similar to that of the laterals. Godwin-Austen (1889–1914) gave an accurate description and drawings of the teeth. According to his drawings the morphology of the teeth of *E. pinacis* is typical for the genus *Endothyrella*, i.e. the central tooth is larger than the ectocones of the first laterals, and the marginals are tricuspid with deep incisions between the two innermost cusps.

**Distribution.** All museum samples examined were collected from Sikkim. Benson's (1860) locality in the Khasi Hills is probably incorrect (Figure 11).

### *Endothyrella plectostoma* (Benson, 1836)

Figures 6D, 13A–B, 19E–F, 20D–E, 22A, 22D–F, 26

1836 *Helix* (*Helicodonta*) *plectostoma* Benson: Journal of the Asiatic Society of Bengal, 5: 351. [not specified. “North-East Frontier of Bengal” (in the title)].

1848 *Helix plectostoma*, — Pfeiffer, Martini & Chemnitz, 1(12): 367, Plate 64, figs 19–21.

1854 *Helix plectostoma*, — Reeve: Conchologia Iconica 7, species 782.

1860 *Helix plectostoma*, — Benson: The Annals and Magazine of Natural History, 3 (5): 247.

1865 *Helix plectostoma*, — W. Blanford: Journal of the Asiatic Society of Bengal 34 (2): 94. [“...the Himalayan and Khasi *H. plectostoma*, Bens. abounded south of the town of Bassein in several places, Pyema Khyoung, Long Island, &c. It was also found by Captain Ingram in Arakan, near Tongoop.”].

1872 *Helix* (*Plectopylis*) *plectostoma*, — Hanley & Theobald: Conchologia Indica...: 7, Plate 13, fig. 2. [“Darjiling and Khasia Hills”].

1875 *Plectopylis plectostoma*, — Godwin-Austen: Proceedings of the Zoological Society of London: 612–613, Plate 73, figs 2–2a. (1874, part IV, published in 1875; see Duncan 1937).

1878 *Helix* (*Plectopylis*) *plectostoma*, — Nevill: Hand list of Mollusca in the Indian Museum...: 1: 71. [“Nágá Hills”, “Bassein, &c., Pegu”, “Sylhet”, “Arakan Hills”, “Khasi Hills”, “Darjeeling”].

1887 *Helix* (*Plectopylis*) *plectostoma*, — Tryon: Manual of Conchology..., 2 (3): 160–161, Plate 34, figs 69–70.

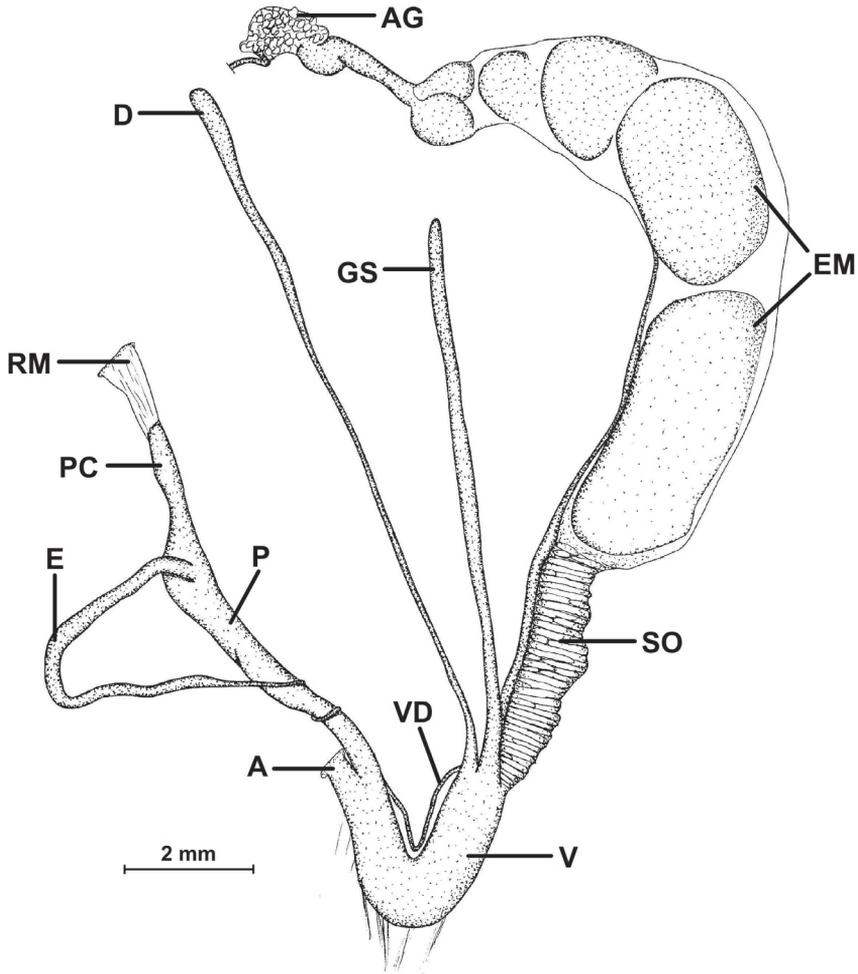
1894 *Plectopylis plectostoma*, — Pilsbry: Manual of Conchology..., 2 (9): 146.

1897b *Plectopylis plectostoma*, — Gude: Science Gossip, 3: 274–275, figs 39a–7c. [“Darjeeling”, “Burma— Bassein and Arakan; Assam — Sylhet, Khasia and Naga Hills”, “Dafla Hills in Assam”].

- 1899c *Plectopylis (Endothyra) plectostoma*, — Gude: Science Gossip, 6: 148, 149.  
 1899d *Plectopylis (Endothyra) plectostoma*, — Gude: Science Gossip, 6: 175, 177.  
 1914b *Plectopylis (Endothyra) plectostoma*, — Gude: The Fauna of British India...: 72, 73, 75, 81–83, figs 31a–c. [“Naga Hills”, “Dafla Hills, Khasi Hills”, “Burma: Arakan Hills”, “Tongoop”, “Bassein: Pegu”, “Sylhet”, “Sikkim : Darjeeling”].  
 1922 *Plectopylis (Endothyra) plectostoma*, — Ehrmann: Sitzungsberichte der Naturforschender Gesellschaft zu Leipzig, 45–48: 8–10.  
 1960 *Plectopylis (Endothyrella) plectostoma*, — Zilch: Handbuch der Paläozoologie, 6 (2): fig. 2092.

**Types.** Darjeeling, coll. MacAndrew ex coll. Benson, UMZC 102160 (7 syntypes of *plectostoma*); Darjeeling, coll. MacAndrew ex coll. Benson, UMZC 102155 (1 syntype of *plectostoma*, Figure 13A); Bengal, coll. MacAndrew ex coll. Benson, UMZC 102156 (3 syntypes of *plectostoma*).

**Additional material examined.** Indien, Khasi Hills, ex coll. Oberwimmer, NHMSB 122805–122810/5; India, Meghalaya, Khasi Hills, Altonaer Museum, ZMH 45909/4; Assam, coll. Steenberg, ZMUC-GAS-1812/2; Naraindher, Cachar, Ede, coll. Godwin-Austen, NHMUK 1903.7.1.1666/15 (several of them are juveniles); Darjiling, coll. W. Blanford, NHMUK 1860.6.27.10/2; India, NHMUK 20150169/1; Teria Ghat, NHMUK 1888.12.4.1536–1540/5; Pegu, coll. Godwin-Austen, NHMUK 1909.3.15.92/7; Naga Hills, coll. Godwin-Austen, NHMUK 1903.7.1.760/3; Pegu, Arakan, NHMUK 1903.7.1.758/3; Arakan, coll. W. Blanford, NHMUK 1909.3.15.60/3; Assam, Khasi Hills, coll. Salisbury ex coll. Beddome, NHMUK 20150170/3; Lhota Naga, coll. Chennell, NHMUK 1903.7.1.759/10; Saddia, E Assam, coll. Godwin-Austen, NHMUK 1903.7.1.761/8; Picholanulla, Durrang, Assam, coll. Godwin-Austen, NHMUK 1903.7.1.763/1; Khasi Hills, coll. W. Blanford, NHMUK 1906.2.2.356.1–3 (3 shells; mixed sample with *E. sowerbyi*: 1906.2.2.356.4); Arakan, coll. W. Blanford, NHMUK 1906.2.2.355/4; India, NHMUK 20150171 (6 specimens); Darjiling, NHMUK 1906.2.2.142/1 (mixed sample with *E. blanda*); Shiroifurar, Lahupa Naga, coll. Godwin-Austen, NHMUK 1903.6.1.762/1; India, NHMUK 71.9.23.206/3; no data, coll. W. Blanford, NHMUK 20150172/2; Muniapur valley, Bishenpur, west side, NHMUK 20150173/25 (several of them are juvenile shells); N. Cachar, coll. Godwin-Austen, NHMUK 20150174/2; Teria Ghat, coll. Godwin-Austen, NHMUK 20150175/1; Cherra, Khasi Hills, Assam, coll. Godwin-Austen, NHMUK 20150176/25; Dunsiri valley, coll. Godwin-Austen, NHMUK 20150177/4; Khasi Hills, coll. Godwin-Austen, NHMUK 20150178/68; Garo Hills, NHMUK leg. W. Robert, coll. Godwin-Austen, NHMUK 20150179/27; Burma, Bassein, coll. Benson 1863, NHMUK 1954.6.2.287/1; Khasi Hills, NHMUK 20150180/1 (mixed sample with *E. tricarinata*: NHMUK 20150181); Khasi Hills, NHMUK 20150182/3; Burroi Gorge, NHMUK 20150183/2; label not readable, NHMUK 20150185/7; Burralli, NHMUK 20150186/10; Khasi Hills, coll. Godwin-Austen, NHMUK 20150187/65; Khasi Hills, coll. W. Blanford, NHMUK 20150188/3; W. Khasi Hills, coll. Godwin-Austen, NHMUK 20150189/1; N. Khasi, coll. Godwin-Austen, NHMUK 20150190 (more



**Figure 26.** Genital anatomy of *Endothyrella plectostoma* (Benson, 1836). For locality, see Figs 19E–F. Abbreviations: **A** atrium **AG** albumen gland **D** diverticulum **E** epiphallus **EM** embryos **GS** gametolytic sac **P** penis **PC** penial caecum **RM** retractor muscle **SO** spermooviduct **V** vagina **VD** vas deferens.

than 100 shells); Khasi Hills, coll. Kennard, NHMUK/20150195/2 (mixed sample with *E. tricarinata*); Manipur, station 36, Godwin Austen Collection. NHMUK 20150191/87; Manipur, station 48, Godwin Austen Collection. NHMUK 20150192/58; Manipur, station 54, Godwin Austen Collection. NHMUK 20150193/119; Manipur, station 54, Godwin Austen Collection. NHMUK 20150194/89; Indien, leg. Stoliczka, coll. Oberwimmer, NHMW 71640/O/415 (2 shells; mixed sample with *E. sowerbyi*: NHMW 109252); Khasi Hills, leg. Stoliczka, 1870, NHMW 92588/3; Viaggio in Birmania (= trip to Burma), Shweego, coll. Fea, 1885–1889, NHMW 20034/4; Shwegoo, Birmania, leg. Mission L. Fea 1885–1889, MNHN 2012-27053/3; Khasi Hills, Himalaya, India, coll. Rušnov ex coll. Blume, NHMW 71770/R/13 (2 adult, 1 juv. shells); Ostindien,

Pegu, leg. Stoliczka, coll. Edlauer, 477, NHMW 75000/E/4770 (1 shell; mixed sample with *E. sowerbyi*: NHMW 109253); Darjeeling, Himalaya, India, coll. Rušnov ex coll. Blume, NHMW 71770/R/14 (1 adult, 1 juv. shells; mixed sample with *E. sowerbyi*: NHMW 71770/R/15); Ostind., coll. Gerstenbrandt, NHMW 83901/G/2745 (2 shells); Pegu, ex coll. Hauer, NHMW 21617/4; Assam, coll. Landauer, NHMW 92594/2; Khasi Hills, Pegu (2 different label were found in the sample), coll. Stoliczka, NHMW 92591/41 (one of them is probably a juvenile *E. tricarinata*); Khasi, leg. Stoliczka, 1880, NHMW 92592/7; Khasi Hills, leg. Stoliczka, 1880, NHMW 92593/2 (mixed sample with *E. sowerbyi*: NHMW 109254 and *E. blanda*: NHMW 109255); East India, leg. Bernardi, Altonaer Museum, coll. O. Semper, ZMH 45908/1; Siam, Altonaer Museum, ZMH 45910/2; Birma, Moulmein, Hinterindien, coll. Krüper 1928, ex coll. Oberwimmer, SMF 118090/2 (mixed sample with *E. sowerbyi*: SMF 346406); Darjeeling, Himalaya, coll. Jetschin ex coll. Oberwimmer 1899, SMF 118088/1 (mixed sample with *E. sowerbyi*: SMF 346407); Khasi Hills, coll. Bosch, ex coll. Rolle, SMF 172072/1 (mixed sample with *E. sowerbyi*: SMF 346408); S-Shan Staaten, Ywathit, Prov. Karenni, a. mittleren Salwen, leg. Michelitz, SMF 150108/3; Indien, coll. Jetschin ex coll. Oberwimmer 1899, SMF 118089/2; Indien, Darjeeling, (alte Schau-sammlung), coll. Kobelt, SMF 150109/2; Khasi-Berge, coll. C. R. Boettger 1904, SMF 118091/1 (Fig. 13B); Assam, coll. Bosch, ex coll. Rolle, SMF 172071/4; Indien, Khasi-Hills, coll. Webb 1928, SMF 150086/2; Indien, Katschar, coll. Möllendorff, Orig. Handb. Pal. Fig. 2092; SMF 150106/4; Goramarah (Ghoramara), Chittagong, coll. Foulon 1936, MNHN 2012-27045/2; no locality, coll. Jousseume, MNHN 2012-27050/3; no locality, coll. Jousseume, MNHN 2012-27049/50.

**Diagnosis.** A very small, sinistral species with very narrow umbilicus, conical dorsal surface, and hairs standing in five rows on the body whorl; palatal plicae more or less straight, the 4th and 5th divided; lamella slightly curved, with short lower and long upper elongation in anterior direction; there are two denticles posteriorly, one above and one below.

**Measurements** (in mm): D: 8.1–9, H: 4.6–5.1 (n = 3, SMF 172072).

**Differential diagnosis.** *Endothyrella plectostoma* is similar to *E. affinis* and *E. tricarinata* in the narrow umbilicus. All other *Endothyrella* species of similar size have wider umbilicus. *Endothyrella plectostoma* is usually smaller, darker than *E. affinis*, it has a horizontal, relatively long plica anterior to the lamella, and has the periostracal folds arranged on five spiral line. In contrast, *E. affinis* lacks the horizontal parietal plica and has four hair rows. Moreover, *E. plectostoma* has a narrower umbilicus and more elevated spire than *E. affinis*. See also under *E. sowerbyi* and *E. tricarinata* and Table 5.

**Description of the genitalia** (Figures 22A, 22D–F, 26): Three specimens have been anatomically examined. Collection data: Sikhim, leg. Godwin-Austen, NHMUK 1903.7.1.451. All specimens had 5–6 embryos developing in their uterus. In one specimen no epiphallic differentiation was observed, the vas deferens started from the distal part of the penis (Fig. 22D).

The left ommatophoral retractor passes between penis and vagina. Atrium short; penis relatively short, internally with holes of various sizes; some tiny, rounded calcareous crystals

were found in the penis lumen, not directly associated with the holes; this inner structure continued in the epiphallus; penial caecum short, with central thickening; retractor muscle short, it inserts on the proximal end of the penial caecum; epiphallus slightly longer than penis, it enters the proximal penial portion laterally; vas deferens long and slender; vagina approximately as long as the penis, but thicker, curved centrally; vagina with several thick and relatively long muscle fibres attaching it to the body wall and to the diaphragm, especially at its curved portion; vagina internally with longitudinal folds, which are rather sharp, elevated at the curved area of the vagina, and low elsewhere; the gametolytic sac and the diverticulum are aligned in parallel; the gametolytic sac is slightly thicker and shorter; a relatively long part of the spermiduct was visible distal to the thickened uterus with the developing embryos; the embryo sac contained no visible calcareous granules, which were reported in other plectopylid species (Páll-Gergely and Hunyadi 2013, Páll-Gergely and Asami 2014); albumen gland conspicuously small. The latter trait is largely dependent on the period of the life cycle of the dissected specimen. In the present case, however, three specimens were anatomically examined and all specimens had a small albumen gland.

**Radula** (Figure 19E–F): Radula elongated, but not very slender, central tooth present, laterals 8, standing in straight lines (perpendicular to the central column); marginals at least 14, staying in oblique rows; central tooth relatively narrow-based triangular, smaller than the endocone of the first lateral, but much larger than the ectocone; laterals bicuspid, endocone oval or narrow-based triangular; marginals tricuspid (the endocone has two cusps); all cusps pointed, the incision between the innermost two cusps is deep; in some cases the three cusps are almost of the same size.

**Distribution.** Museum samples are labelled from several locations. This species is probably widely distributed in north-eastern India through south-eastern Bangladesh to Bago, the Arakan Hills and in the Kayah State in Burma (Myanmar) (Figure 7). A sample (ZMH 45910) was collected in “Siam” (= Thailand), which is possible because other samples were collected in Myanmar not far from the Thai Border.

**Remarks.** The name “*prodigium* Benson” probably refers to *Endothyrella plectostoma*. It is a manuscript name, which was mentioned several times in the literature (Godwin-Austen 1875, Tryon 1887, Pilsbry 1894, Gude 1899c), but has never been published formally.

***Endothyrella robustistriata* Páll-Gergely, sp. n.**

<http://zoobank.org/ED59E23B-D8CF-4E09-A439-FE7919DDD5F7>

Figures 9K–L, 23C–D

1914b *Plectopylis* (*Endothyra*) *minor* (partim), — Gude: The Fauna of British India...: 76.

**Type material.** Manipur, Laisen Peak, coll. Godwin-Austen, NHMUK 1903.7.1.3453/1 (holotype, Figure 23D); Naga Hills, Ihang valley, coll. Godwin-Austen, NHMUK

1903.7.1.770/3 paratypes; Naga Hills, coll. Godwin-Austen, NHMUK 1903.7.1.767/3 paratypes (Figure 23C); Lhota Naga Hills, coll. Chennell, NHMUK 1903.7.1.765/4 paratypes.

**Diagnosis.** A tiny species with elevated spire, smooth ventral side and strongly reticulated dorsal surface; parietal wall with a single lamella, an upper and a lower denticle posteriorly, and a long lower plica which reaches the peristome.

**Description.** Shell tiny, sinistral, with slightly elevated spire and conical/domed dorsal surface; colour light brown, greenish or yellowish; protoconch consists of approx. 2 whorls, glossy, in some populations (NHMUK 1903.7.1.767, NHMUK 1903.7.1.770, NHMUK 1903.7.1.3453) only the last half whorl has a somewhat ribbed surface, whereas in another population (NHMUK 1903.7.1.765) nearly the whole protoconch is ribbed; dorsal surface of the teleoconch with clearly visible reticulated sculpture dominated by spiral lines; ventral side hairless, smooth, glossy, sometimes with radial growth lines; the ventral and dorsal surface change relatively abruptly above the middle line of the body whorls (from apertural = frontal view); inside the umbilicus there are sharp periostracal folds corresponding with radial ribs; whorls 4.5–4.75 ( $n = 3$ ), slowly growing, separated by relatively deep suture; umbilicus narrow and deep; apertural lip whitish, thickened, normally not reflexed, or reflexed only near the umbilicus; callus very weak, nearly invisible in case of fresh shells, in case of old, corroded shells it becomes white; aperture without entering fold.

Two opened specimens were observed (NHMUK 1903.7.1.767 and NHMUK 1903.7.1.765). Parietal wall with one rather straight lamella which bends anteriorly; it has both the upper and lower ends elongated anteriorly; two small denticles visible at the posterior side of the lamella, one above and one below; lower plica very long, reaches the peristome; palatal wall with six plicae; first slim and short, the second–fifth plicae horizontal; they do not seem to be divided if we observe through the translucent shell wall, but their middle portion (where the lamella is present on the parietal wall) is much lower; the posterior ends of the middle plicae slightly bent downwards, whereas the anterior parts are straight and horizontal; the last plica is short and slightly curved (Figure 9K–L).

**Measurements** (in mm): D: 4.1–4.6, H: 2.3–3.5 ( $n = 2$  NHMUK 1903.7.1.765).

**Differential diagnosis.** *Endothyrella blanda* is similar in shell shape to *E. robustistriata* sp. n., but is larger, has hairy ventral surface (or if hairs are missing, than hollows are visible indicating the hairs' positions), and on its dorsal surface the radial lines are dominant. See also under *E. macromphalus* and *E. williamsoni* and Table 5.

**Etymology.** The word *robustistriata* means strongly striated (Latin) which refers to the prominent spiral striae of the new species on the dorsal side of its shell.

**Type locality.** Muniapur, Laisen Peak.

**Distribution.** The new species is known only from the Naga Hills and Manipur (Figure 11).

***Endothyrella sowerbyi* (Gude, 1899)**

Figure 13C–D

1899a *Plectopylis sowerbyi* Gude: Science Gossip, 5: 239, figs 93a–f. [“Khasi Hills: Assam”].

1899c *Plectopylis (Endothyra) sowerbyi*, — Gude: Science Gossip, 6: 148, 149.

1899d *Plectopylis (Endothyra) sowerbyi*, — Gude: Science Gossip, 6: 175, 177.

1914b *Plectopylis (Endothyra) sowerbyi*, — Gude: The Fauna of British India...: 72, 80–81, figs 30a–f.

1915 *Plectopylis (Endothyra) sowerbyi*, — Gude: Records of the Indian Museum, 8: 507, 509.

**Types.** Khasia Hills, India, NHMUK 1922.8.29.48. (holotype, Figure 13C).

**Additional material examined.** Indien, leg. Stoliczka, coll. Oberwimmer, NHMW 109252/2 (mixed sample with *E. plectostoma*: NHMW 71640/O/415); Ostindien, Pegu, leg. Stoliczka, coll. Edlauer, 477, NHMW 109253/7 (mixed sample with *E. plectostoma*: NHMW 75000/E/4770); Darjeeling, Himalaya, India, coll. Rušnov ex coll. Blume, NHMW 71770/R/15 (3 shells; mixed sample with *E. plectostoma*: NHMW 71770/R/14); Khasi Hills, leg. Stoliczka, 1880, NHMW 109254 (approx. 70 shells; mixed sample with *E. plectostoma*: NHMW 92593 and *E. blanda*: NHMW 109255); Khasi Hills, coll. W. Blanford, NHMUK 1906.2.2.356.4 (3 shells; mixed sample with *E. plectostoma*: NHMUK 1906.2.2.356.1–3); Darjeeling, 3500', leg. Lister, NHMUK 1907.9.13.11–22/11; Birma, Moulmein, Hinterindien, coll. Krüper 1928, ex coll. Oberwimmer, SMF 346406/2 (mixed sample with *E. plectostoma*: SMF 118090); Khasi Hills, coll. Bosch, ex coll. Rolle, SMF 346408/5 (mixed sample with *E. plectostoma*: SMF 172072) (Fig. 13D); Khasi Hills, coll. Jetschin, ex coll. Linter 1893, SMF 118087/1; Darjeeling, Himalaya, coll. Jetschin ex coll. Oberwimmer 1899, SMF 346407/2 (mixed sample with *E. plectostoma*: SMF 118088).

**Diagnosis.** A very small, sinistral species with narrow umbilicus (but wider than in the three similar species; *affinis*, *plectostoma*, *tricarinata*), rather domed dorsal surface, and hairs standing in five rows on the body whorl; the hairs are usually missing and the ventral side is with relatively strong radial lines; plication similar to *E. plectostoma*, but the main anterior parietal plica is missing or weak.

**Measurements** (in mm): D: 7.8–8.6, H: 4.3–5.0 (n = 3, SMF 346408).

**Differential diagnosis.** *Endothyrella affinis* is larger, has lighter shell with narrower umbilicus and a weaker sculpture. *Endothyrella sowerbyi* has a wider umbilicus and a thinner peristome than *E. plectostoma*. Moreover, the spire is lower and the dorsal side is rather domed in *E. sowerbyi* (conical in *plectostoma*), and the main parietal plica is weaker or missing. See also under *E. tricarinata* and Table 5.

**Distribution.** Museum specimens are collected from the Khasi Hills, Darjeeling, and Burma.

**Remarks.** During the preparation of this revision, *Endothyrella sowerbyi* was handled as the synonym of *E. plectostoma*, because the only known specimen (the holo-

type) looked like a juvenile shell of *E. plectostoma*. The first author recognized that *E. sowerbyi* is a valid species in the Senckenberg Museum in August, 2015, because of several mixed samples deposited there. Thus, the *Endothyrella plectostomalsowerbyi* sample of the SMF were identified and the *E. sowerbyi* shells were separated by B. Páll-Gergely. The *E. plectostoma* samples in the NHM were checked by Jonathan Ablett, whereas those in the NHMW were examined by Zoltán Fehér.

### *Endothyrella tricarinata* (Gude, 1897)

Figure 13E–F

1897b *Plectopylis plectostoma* var. *tricarinata* Gude: Science Gossip, 3: 275, figs 40a–b. [“Bengal”].

1897g *Plectopylis plectostoma* var. *tricarinata*, — Gude: The Journal of Malacology, 6: 45, fig. 2.

1899c *Plectopylis (Endothyra) plectostoma* var. *tricarinata*, — Gude: Science Gossip, 6: 148.

1899d *Plectopylis (Endothyra) plectostoma* var. *tricarinata*, — Gude: Science Gossip, 6: 176, 177.

1901 *Plectopylis plectostoma* var. *exerta* Gude **new synonym**: The Journal of Malacology, 8: 49, figs 5a–d. [“Khasi Hills: Assam”].

1914b *Plectopylis (Endothyra) plectostoma* var. *tricarinata*, — Gude: The Fauna of British India...: 83, figs 32a–b. [“Bengal”, “Khasi Hills”].

1914b *Plectopylis (Endothyra) plectostoma* var. *exerta*, Gude, The Fauna of British India...: 83–84, figs 33a–d.

**Types.** Bengal, coll. MacAndrew ex coll. Benson, UMZC 102170 (2 syntypes of *Plectopylis plectostoma* var. *tricarinata*, Figure 13E); Khasia Hills, ex Nissor (?), NHMUK 1922.8.29.50. (syntype of *Plectopylis plectostoma* var. *exerta*, Figure 13F).

**Additional material examined.** India, Khasia Hills, K4.30, coll. Rolle, NHMW 50854/2; Assam, Khasia Hills, coll. Bosch, ex coll. Rolle, SMF 172073/3; Assam, Cherpooonjee, coll. Jetschin, ex coll. Gude 1900, (labelled as syntype, but it is probably not), SMF 118097/1; Assam, coll. Ehrmann ex coll. Schlüter, SMF 150113/1; Khasi Hills, figured in Godwin-Austen (1874), NHMUK 1903.7.1.757 (note that in the original sample it is erroneously 759) (11 specimens under the name *affinis*); Khasi Hills, coll. W. Blanford, NHMUK 1906.1.1.743/2; Khasi Hills, India, Assam, NHMUK 1916.3.16.6–7/2; Khasi Hills, coll. Kennard, NHMUK 20150181/2 (mixed sample with *E. plectostoma* see NHMUK 20150180); Khasi Hills, NHMUK 20150196/2 (mixed sample with *E. plectostoma*); Khasi Hills, Assam, ‘Preston’, V.W. MacAndrew Collection (Acc. No.1563), NHMUK 20150197/3; Khasi Hills, Bengal, ‘Rolle, C/R June 03’, V.W. MacAndrew Collection (Acc. No.1563), NHMUK 20150198/2; Khasi Hills, India, ‘Rolle, C/R 8/5/13’, V.W. MacAndrew Collection (Acc. No.1563), NHMUK 20150199/2.

**Diagnosis.** A small, sinistral species with narrow umbilicus, conical dorsal surface with strong spiral lines, strongly, densely ribbed surface, and hairs standing in four

rows on the body whorl; palatal plicae more or less straight, they are more or less divided; lamella slightly curved, with small denticles on the posterior side (they might fuse to the lamella), and a long upper plica on the anterior side of the lamella.

**Measurements** (in mm): D: 10.1–10.4, H: 6.3–6.7 (n = 2, SMF 172073).

**Differential diagnosis.** *Endothyrella affinis* has less shouldered whorls, wider umbilicus, weaker sculpture and it lacks the long horizontal plica anterior to the lamella. *Endothyrella tricarinata* differs from *E. plectostoma* by the larger size, more conical dorsal surface, narrower umbilicus, the shouldered whorls, the presence of only four rows of hairs, and the stronger sculpture. *Endothyrella sowerbyi* has much weaker dorsal sculpture and has wider umbilicus. See also Table 5.

**Distribution.** All museum samples were collected from the Khasi Hills and Assam (Figure 11).

**Remarks.** Two varieties of *Plectopylis plectostoma* have been described under the names *Plectopylis plectostoma* var. *tricarinata* and *P. plectostoma* var. *exerta*. Both of them differ from typical *Endothyrella plectostoma* specimens by the more shouldered whorls, and the more conical dorsal side of the shell having stronger spiral lines. No difference between the type specimens of these forms have been found except for the presence (*exerta*) and the absence (*tricarinata*) of hairs. The absence of hairs might be due to the corroded state of the syntypes of *tricarinata*. Although the difference between typical *E. plectostoma* and typical *tricarinata/exerta* shells seem to be minor, we found no intermediate forms, and in some cases we found mixed museum samples which indicate that the shells might have been collected from the same site. This suggest that *Endothyrella plectostoma* and *E. tricarinata* are distinct species.

### *Endothyrella williamsoni* (Gude, 1915)

Figure 17A

1915 *Plectopylis (Endothyra) williamsoni* Gude: Records of the Indian Museum, 8: 509, Plate 42, figs 1a–d. [“Abor Hills, exact part not indicated”].

**Types.** Abor Hills, leg. C.F.G. Oakes, R.E., NHMUK 1903.7.1.3087. (5 syntypes, Figure 17A)

**Diagnosis.** Shell very small, sinistral with narrow umbilicus and conical dorsal surface; shell hairless but densely, finely ribbed and ornamented with low radial periostracal lamellae on the whole shell; callus strong; palatal plicae horizontal, almost straight and thin at their middle; lamella slightly curved; there is long, horizontal plica anteriorly to the lamella, and a short horizontal plica above the long one; additionally, there is a very short upper plica above the lamella, a small denticle posteriorly above, and a long lower plica near the suture which reaches the aperture.

**Measurements** (in mm): D: 6, H: 3.6–3.7 (n = 2, type series).

**Differential diagnosis.** *Endothyrella williamsoni* has a more elevated spire than *E. macromphalus* and *E. minor*, and has two horizontal parietal plicae anterior to the

lamella which are missing in the other two species. The most similar species in terms of shell shape and size to *E. williamsoni* is *E. blanda*. The latter species, on the other hand, lacks the two horizontal parietal plicae anterior to the lamella which area characteristic for *E. williamsoni*. Moreover, *E. blanda* specimens have seven rows of hairs, whereas *E. williamsoni* is hairless. *Endothyrella robustistriata* sp. n. is smaller, has stronger dorsal sculpture and lack the main plica which is characteristic for *E. williamsoni*. See also Table 5.

**Distribution.** This species is known from the type locality only (Figure 10).

### Species with uncertain identity

#### *Plectopylis hanleyi* Godwin-Austen, 1879b

1879b *Plectopylis hanleyi* Godwin-Austen: The Annals and Magazine of Natural History, 5 (4): 164. [“Sikkim?”].

1897c *Plectopylis hanleyi*, — Gude: Science Gossip, 4: 11.

1899a *Plectopylis hanleyi*, — Gude: Science Gossip, 5: 240.

1899c *Plectopylis (Endothyra) hanleyi*, — Gude: Science Gossip, 6: 148.

1899d *Plectopylis (Endothyra) hanleyi*, — Gude: Science Gossip, 6: 175, 176.

1914b *Plectopylis (Endothyra) hanleyi*, — Gude: The Fauna of British India...: 73, 77.

**Original description.** “Shell sinistral, depressedly conoid, openly umbilicated, probably hirsute when young. Sculpture coarse, irregular, transverse ridges. Colour uniform ochraceous. Spire conoidal; apex blunt, smooth. Suture well marked. Whorls six, close-wound, convex. Aperture semicircular, diagonal; peristome somewhat thickened, white, with a thin callus on the parietal margin, not to the extent of a ridge. Size — major diam. 5.5, minor diam. 5.0, alt. 3.0 millims. Parietal vertical lamina simple; palatal plicæ in two rows, four long in front, four short behind, and one basal long. The shell is very distinct; it has somewhat the form of *P. plectostoma*, but is not so angular on the periphery, while the internal plication is quite different, besides being so very much smaller in size.”

**Remarks.** In the original description Godwin-Austen (1879b) wrote that the holotype is “in the collection of Mr. Sylvanus Hanley”. In Godwin-Austen’s copy of Gude (1914, page 77), Godwin-Austen has written “In my collection”. The holotype, however, was not found in the collection of the NHM. Only one NHM specimen was found labelled *Plectopylis hanleyi*, and this is annotated with a question mark (“Sikkim, Rarhichu, H. H. Godwin-Austen colln.”). However, this specimen is very similar to the type specimen of *Plectopylis blanda*, and is not identical with the single shell in Godwin-Austen’s (1879b) description, because it has only 4.75 whorls (the holotype of *P. hanleyi* has six). Moreover, Godwin-Austen (1879b) described the palatal lamellation, whereas the above mentioned specimen is intact, therefore the inner lamellae and plicae could not be observed. Some parts of Hanley’s collection are housed in the

Leeds Museum and in the Manchester Museum. The former were contacted and confirmed that the holotype was not deposited there. The catalogue of the type specimens of the Manchester Museum (McGhee 2008) did not list *Plectopylis hanleyi*. Since the holotype of *Plectopylis hanleyi* seems to be lost, and the description is not sufficient to diagnose the species (although it matches with *E. blanda*), *P. hanleyi* is considered to be a nomen dubium.

## Results and discussion

Examining all species assigned to *Chersaecia* and *Endothyrella* by Gude (1899c, 1915) revealed that all species formerly assigned to *Endothyrella* by Gude (1899c, 1915) were correctly placed in that genus. The genus *Chersaecia* is, on the other hand, very diverse in terms of shell characters. The type species of *Chersaecia*, *Plectopylis leiophis*, has a finely tuberculated protoconch and an apertural fold (Figure 2). We suggest retaining only those species in *Chersaecia* which share the same features. Consequently, some former *Chersaecia* species (*aborensis*, *andersoni*, *babbagei*, *bedfordi*, *brahma*, *laomontana*, *oglei*, *serica*, *williamsoni*) are excluded from that genus. Most of these species (*aborensis*, *babbagei*, *bedfordi*, *brahma*, *oglei*, *serica*, *williamsoni*) are classified in *Endothyrella* on the basis of the absence of an apertural fold, the ribbed protoconch, the hairs standing in multiple spiral lines and the characters of the armature. *Plectopylis andersoni* and *P. laomontana* are not assigned to either genus because of the large, keeled shell of *andersoni* with reticulated protoconch and the unique anatomical features of *laomontana* (unpublished information). The systematic position of these two species and the species remained in genus *Chersaecia* will be discussed in separate publications.

The finely ribbed protoconch is considered to be one of the key characters allowing separation of *Chersaecia* and *Endothyrella* species. Dextral *Endothyrella* species however, have “no typical” protoconch: (1) *E. babbagei* has slightly waved ribs (Figure 6C); (2) *E. inexpectata* sp. n. has a rather smooth protoconch, some ribbing is only visible on the last half/quarter of whorl (Figure 6F); (3) *E. serica* has a very finely granulated protoconch with rather irregular ribs/ridges and there is an additional spiral line running close to and parallel with the suture (Figures 6B). However, we see no justification for erecting new (sub) genera for these dextral species yet. Information on their anatomy and molecular evidence may shed light on the importance of these differences as well as the relationship with sinistral *Endothyrella* species.

Based on the ribbed protoconch *Endothyrella* seems to be closely related to *Gudeodiscus*, *Halongella*, *Sicradiscus* and *Sinicola*, and to “*Plectopylis*” *laomontana* and “*Plectopylis*” *andersoni*. Other plectopylid genera without ribs on the protoconch (*Plectopylis*, *Endoplona*, *Chersaecia*) are probably only distantly related. The radula morphology of *Endothyrella* (large central tooth and tricuspid, pointed marginals) are similar to *Sinicola*, *Sicradiscus* and *Gudeodiscus* (*Gudeodiscus*) species, whereas *Gudeodiscus* (*Veludiscus*) Páll-Gergely 2015 and *Halongella* are characterized by small central teeth and bicuspid or bluntly tricuspid marginals.

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# Contributions to the knowledge of oribatid mites of Indonesia. I. The genus *Allogalumna* (Galumnidae) with descriptions of two new species (Acari, Oribatida)

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## Abstract

Two new species of oribatid mites of the genus *Allogalumna* (Oribatida, Galumnidae) are described from litter and soil materials of Sumatra, Indonesia. *Allogalumna indonesiensis* **sp. n.** is morphologically most similar to *A. borhidii* Balogh & Mahunka, 1979, *A. quadrimaculata* (Mahunka, 1988), *A. rotundiceps* Aoki, 1996 and *A. plowmanae* Balogh & Balogh, 1983; however, the new species differs by having densely ciliate bothridial heads, larger body size and absence of a median pore. *Allogalumna paranovazealandica* **sp. n.** is morphologically most similar to *A. novazealandica* Hammer, 1968; however, the new species differs by the shorter body length and barbed and curving postero-laterad bothridial setae. The genus *Allogalumna* is recorded for the first time in the Indonesian fauna.

## Keywords

Oribatid mites, *Allogalumna*, new species, new record, Indonesia

## Introduction

At present, the oribatid mite fauna (Acari, Oribatida) of Indonesia is poorly known (Sellnick 1925, 1930; Willmann 1929, 1932; Csiszár 1961; Balogh and Mahunka 1968; Mahunka 1977, 1989, 1990; Hammer 1979, 1981a, 1981b, 1982; Aoki et al. 1994; Niedbala 2007, 2008). This work is a part of a study on Indonesian oribatids and based on material which was collected in 2013 in the framework of the interdisciplinary project “Ecological and socioeconomic functions of tropical lowland rainforest transformation systems (Sumatra, Indonesia)”. Litter and soil samples were taken along a land use gradient including rainforest, jungle rubber, rubber and oil palm plantations in Jambi Province. For more details on the study region and experimental design see Barnes et al. (2014).

This paper includes the data on taxa of *Allogalumna* Grandjean, 1936 (Galumnidae). During taxonomic identification, two new species of this genus were found. The main goal of the paper is to describe and illustrate these species under the names *A. indonesiensis* sp. n. and *A. paranovazealandica* sp. n.

*Allogalumna* is a genus that was proposed by Grandjean (1936) with *Galumna alamellae* Jacot, 1935 as type species. Based on updated generic diagnosis (Ermilov et al. 2013a), it comprises more than 40<sup>1</sup> species collectively having a cosmopolitan distribution; *Allogalumna* has not been reported before in the Indonesian fauna. An identification key to all known species of this genus was given by Akrami (2015), while additional keys to selective species were presented by Balogh and Balogh (2002) and Ermilov and Anichkin (2014).

## Materials and methods

Exact collection locality and habitat are given in the respective “Material examined” section for each new species.

Specimens were mounted in lactic acid on temporary cavity slides for measurement and illustration. The body length was measured in lateral view, from the tip of the rostrum to the posterior edge of the ventral plate. Notogastral width refers to the maximum width in dorsal aspect. Lengths of body setae were measured in lateral aspect. All body measurements are presented in micrometers. Formulae for leg setation are given in parentheses according to the sequence trochanter–femur–genu–tibia–tarsus (famulus included). Formulae for leg solenidia are given in square brackets according to the sequence genu–tibia–tarsus.

General terminology used in this paper follows that of Grandjean (summarized by Norton and Behan-Pelletier 2009).

Drawings were made with a camera lucida using a Carl Zeiss transmission light microscope “Axioskop-2 Plus”.

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<sup>1</sup> Subías (2004, updated 2015) included 37 species in *Allogalumna*.

## Descriptions

### *Allogalumna indonesiensis* sp. n.

http://zoobank.org/2E8C0C04-C670-4191-AA46-3134623A5D09

Figs 1–9

**Diagnosis.** Body size: 282–298 × 215–232. Rostral, lamellar and interlamellar setae minute. Bothridial setae with unilaterally dilated, densely ciliate head. Anterior notogastral margin not developed. Four pairs of porose areas rounded. Median pore absent. Postanal porose area elongate oval.

**Description.** *Measurements.* Body length: 282 (holotype: male), 282–298 (five paratypes: two females and three males); notogaster width: 215 (holotype), 215–232 (five paratypes). Without sexual dimorphism.

*Integument.* Body color brown. Body surface, pteromorphs, subcapitular mentum, genital and anal plates, and legs smooth.

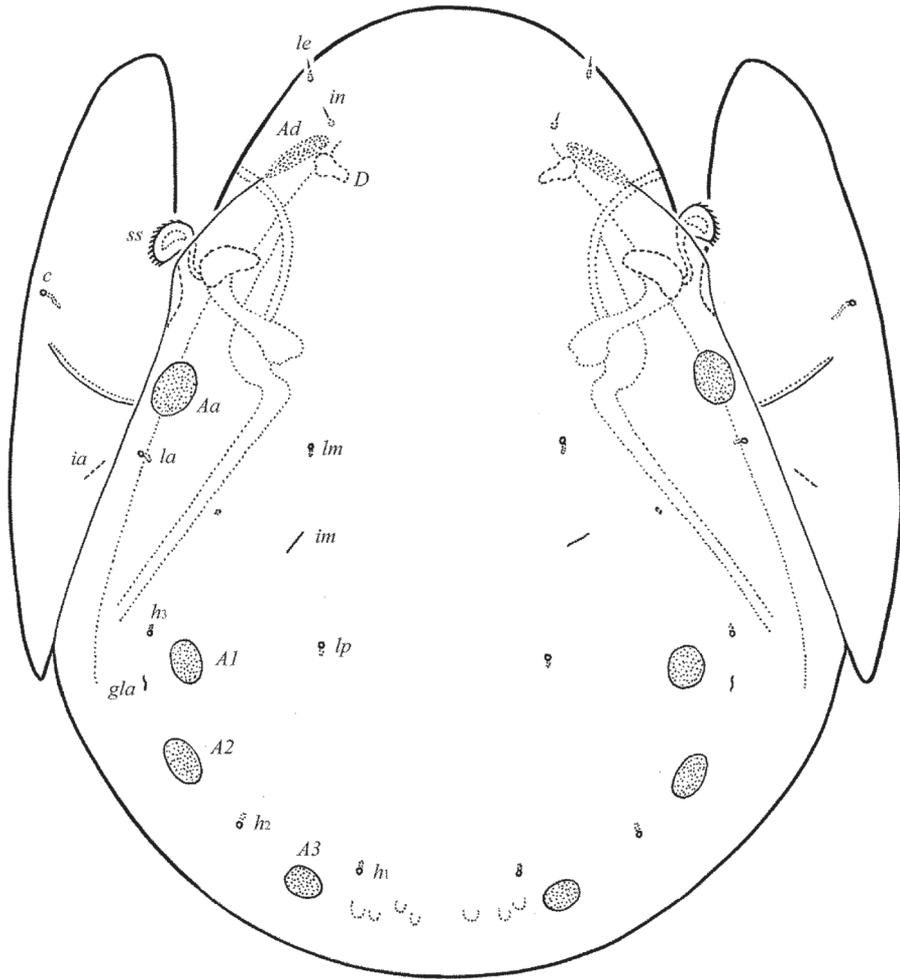
*Prodorsum* (Figs 1, 3, 5). Rostrum broadly rounded. Sublamellar lines (*S*) distinct, curving backwards. Rostral (*ro*), lamellar (*le*) and interlamellar (*in*) setae minute (all 4), thin, smooth. Bothridial setae (*bs*) comparatively short (49–53), with unilaterally dilated, densely ciliate head. Exobothridial setae and their alveoli absent. Porose areas *Ad* elongate oval, transversally oriented (16–20 × 6–8).

*Notogaster* (Figs 1, 3, 4). Anterior notogastral margin not developed. Dorsophragmata (*D*) of medium size, elongated longitudinally. Notogastral setae represented by 10 pairs of alveoli. Four pairs of porose areas rounded, with distinct margins: *Aa* (16–18) usually slightly larger than *A1*, *A2* and *A3* (all 12–16). Setal alveoli *la* inserted posteriorly to *Aa*. Median pore absent in males and females. All lyrifissures (*ia*, *im*, *ip*, *ib*, *ips*) distinct, *im* located between setal alveoli *lm* and *lp*. Opisthonotal gland openings (*gla*) located laterally to *A1*.

*Gnathosoma* (Fig. 6). Morphology of subcapitulum, palps and chelicerae typical for most Galumnidae (for example, see Engelbrecht 1969, 1972; Ermilov and Anichkin 2010, 2011; Ermilov et al. 2011, 2013b; Bayartogtokh and Akrami 2014). Subcapitulum size: 61–69 × 61–69. Subcapitular setae setiform, smooth, *a* (10–12) longer than *m* (6–8) and *b* (4), *a* thickest, *b* thinnest. Two pairs of adoral setae (*or*<sub>1</sub>, *or*<sub>2</sub>, 8) thin, indistinctly barbed. Palps (57) with typical setation: 0–2–1–3–9(+ω). Axillary sacculi (*sac*) distinct. Chelicerae (77) with two setiform, barbed setae; *cha* (28) longer than *chb* (16). Trägårdh's organ long, tapered.

*Epimeral and lateral podosomal regions* (Fig. 2). Anterior tectum of epimere I smooth. Apodemes 1, 2, sejugal and 3 well visible. Four pairs of short (all 4), thin setae, setal formula: 1–0–1–2. Pedotecta II (Pd II) scale-like in lateral view, rounded distally in ventral view. Discidia (*dis*) sharply triangular. Circumpedial carinae (*cp*) distinct, directed slightly laterally to setae *3b*.

*Anogenital region* (Figs 2, 4, 7, 8). Six pairs of genital (*g*<sub>1</sub>, 8; *g*<sub>2</sub>–*g*<sub>6</sub>, 4), one pair of aggenital (*ag*, 4), two pairs of anal (*an*<sub>1</sub>, *an*<sub>2</sub>, 4) and three pairs of adanal (*ad*<sub>1</sub>–*ad*<sub>3</sub>, 4) setae thin, smooth. Two genital setae on anterior edge of each genital plate. Adanal se-

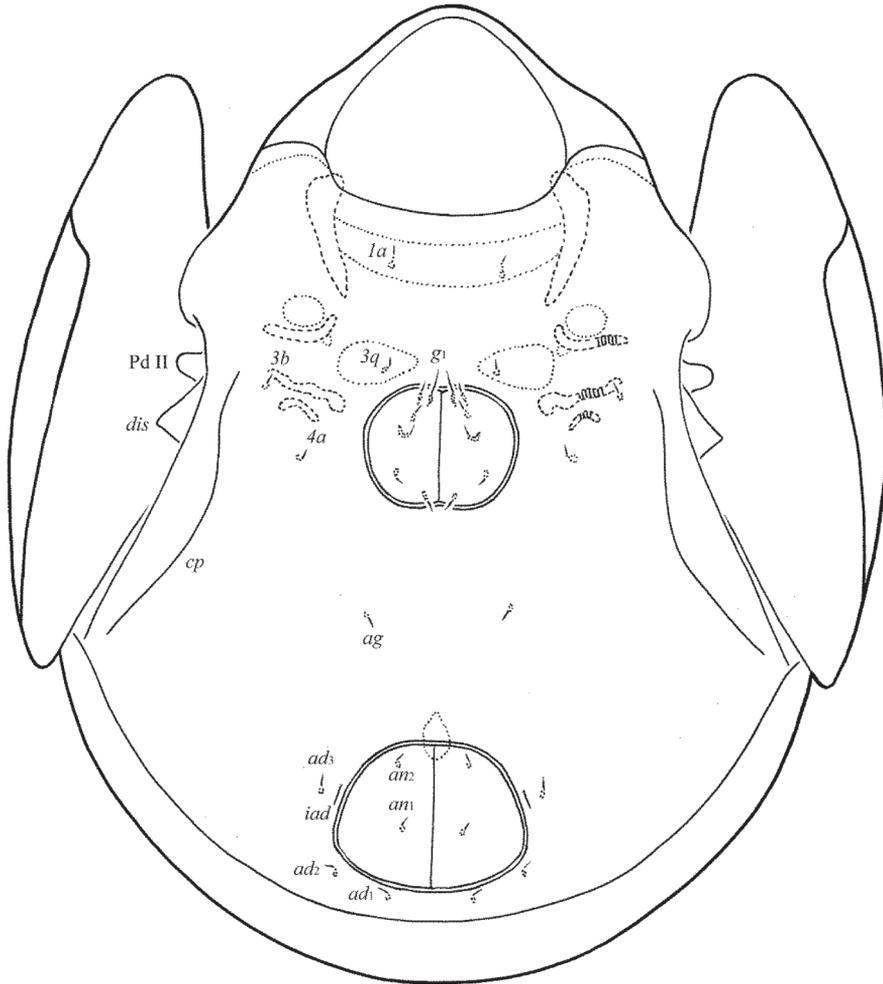


**Figure 1.** *Allogalumna indonesiensis* sp. n., adult: dorsal view. Scale bar 50  $\mu$ m.

tae  $ad_3$  inserted laterally to adanal lyrifissures ( $iad$ ). Postanal porose area ( $Ap$ ) elongate oval, transversally oriented (28–32  $\times$  6–8).

**Legs** (Fig. 9). Morphology of leg segments, setae and solenidia typical for most Galumnidae (for example, see Engelbrecht 1969, 1972; Ermilov and Anichkin 2010, 2011; Ermilov et al. 2011; Bayartogtokh and Akrami 2014). Tridactylous; claws smooth. Formulas of leg setation and solenidia: I (1–4–3–4–20) [1–2–2], II (1–4–3–4–15) [1–1–2], III (1–2–1–3–15) [1–1–0], IV (1–2–2–3–12) [0–1–0]; homology of setae and solenidia indicated in Table 1. Solenidion  $\varphi$  of tibiae IV inserted dorsally at about 2/3 length of segment.

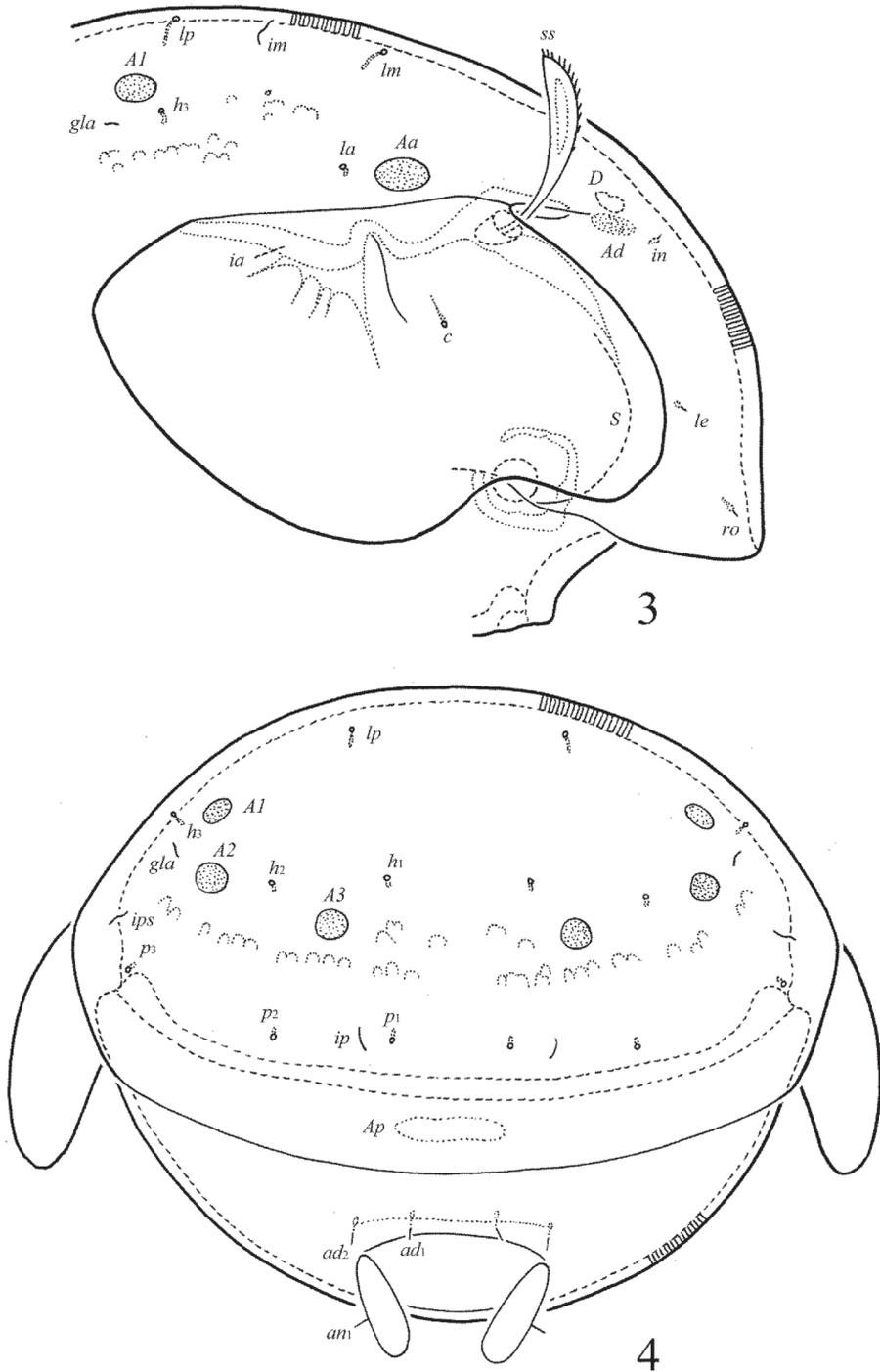
**Material examined.** Holotype (male): Indonesia, Sumatra, Harapan landscape, Jungle rubber agroforest, research site HJ2 (project site number), 01°49'31.9"S, 103°17'39.2"E,



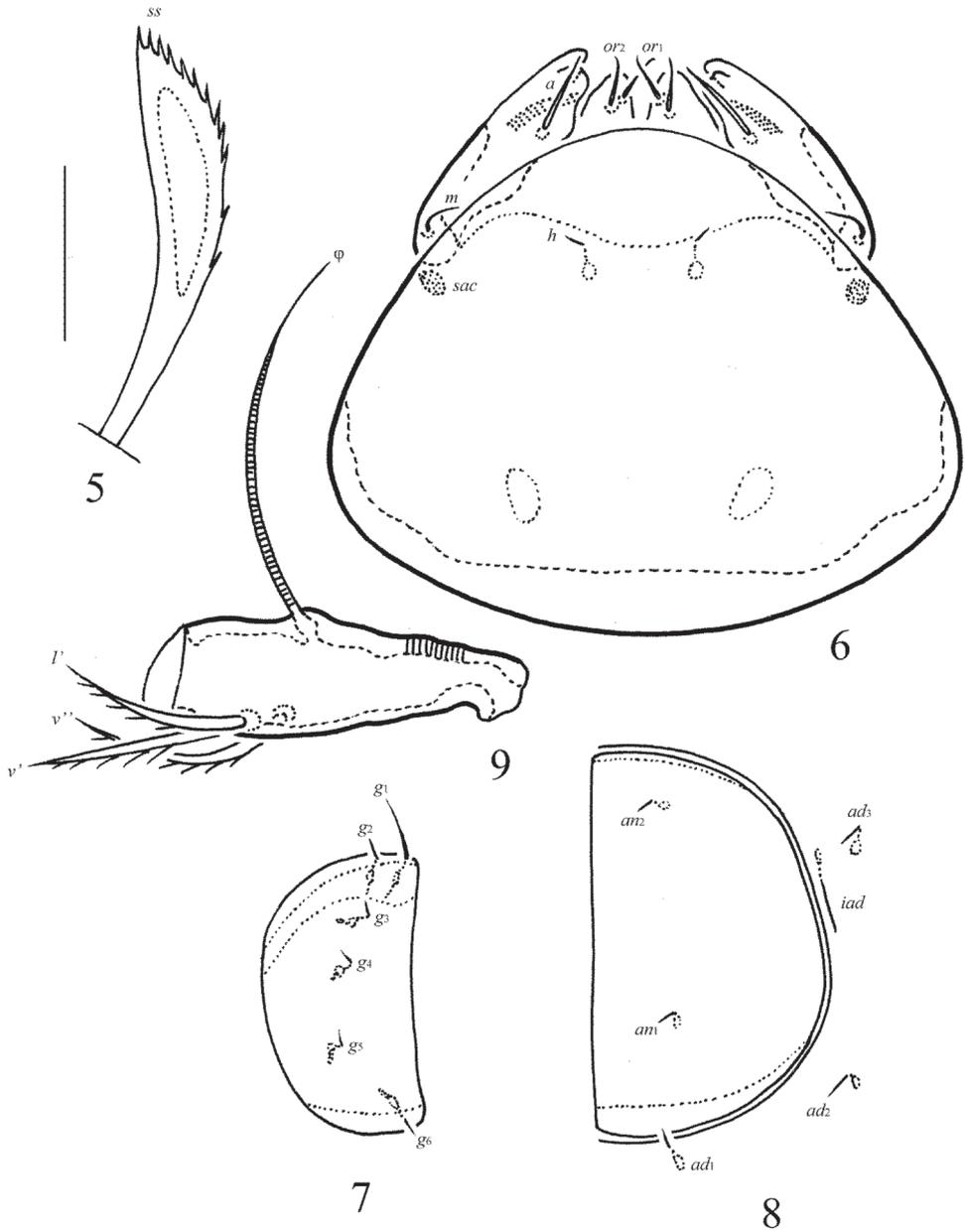
**Figure 2.** *Allogalumna indonesiensis* sp. n., adult: ventral view (gnathosoma and legs not shown). Scale bar 50  $\mu$ m.

84 m a.s.l., from forest floor litter material. Two paratypes (female and male): Indonesia, Sumatra, Bukit Duabelas landscape, secondary rainforest, research site BF1, 01°59'42.5"S, 102°45'08.1"E, 83 m a.s.l., from forest floor litter material. Three paratypes (female and two males): Indonesia, Sumatra, Bukit Duabelas landscape, Jungle rubber agroforest, research site BJ5, 02°08'35.6"S, E 102°51'04.7"E, 51 m a.s.l., from upper soil layer (0–5 cm). All specimens were collected by Bernhard Klärner (15.XI.2013) and determined and collected to morphospecies level by Dorothee Sandmann.

**Type deposition.** The holotype is deposited in LIPI (Indonesian Institute of Science) Cibinong, Indonesia; three paratypes are deposited in the collection of the Senckenberg Museum, Görlitz, Germany; two paratypes are deposited in the collection of the Tyumen State University Museum of Zoology, Tyumen, Russia.



**Figures 3–4.** *Allogalumna indonesiensis* sp. n., adult: **3** anterior part of body, lateral view (gnathosoma and leg I not shown) **4** posterior view. Scale bar 50  $\mu$ m.



**Figures 5–9.** *Allogalumna indonesiensis* sp. n., adult: **5** bothridial seta **6** subcapitulum, ventral view **7** genital plate, right **8** anal plate, left, and adanal setae **9** tibia of leg IV, right, antiaxial view. Scale bar 20  $\mu$ m.

**Table 1.** Leg setation and solenidia of adult *Allogalumna indonesiensis* sp. n. (same data for *A. paranovazealandica* sp. n.)

Leg	Tr	Fe	Ge	Ti	Ta
I	<i>v'</i>	<i>d, (l), bv''</i>	<i>(l), v', ε</i>	<i>(l), (v), φ<sub>1</sub>, φ<sub>2</sub></i>	<i>(ft), (tc), (it), (p), (u), (a), s, (pv), v', (pl), l'', ε, ω<sub>1</sub>, ω<sub>2</sub></i>
II	<i>v'</i>	<i>d, (l), bv''</i>	<i>(l), v', σ</i>	<i>(l), (v), φ</i>	<i>(ft), (tc), (it), (p), (u), (a), s, (pv), ω<sub>1</sub>, ω<sub>2</sub></i>
III	<i>v'</i>	<i>d, ev'</i>	<i>l', σ</i>	<i>l', (v), φ</i>	<i>(ft), (tc), (it), (p), (u), (a), s, (pv)</i>
IV	<i>v'</i>	<i>d, ev'</i>	<i>d, l'</i>	<i>l', (v), φ</i>	<i>ft'', (tc), (p), (u), (a), s, (pv)</i>

Note: Roman letters refer to normal setae, Greek letters to solenidia (except  $\varepsilon$  = famulus). Single prime (') marks setae on the anterior and double prime (') setae on the posterior side of a given leg segment. Parentheses refer to a pair of setae. Tr – trochanter, Fe – femur, Ge – genu, Ti – Tibia, Ta – tarsus.

**Etymology.** The specific name *indonesiensis* refers to the country of origin, Indonesia.

**Remarks.** *Allogalumna indonesiensis* sp. n. is most similar to *A. borhidii* Balogh & Mahunka, 1979 from the Neotropical region (see Balogh and Mahunka 1979), *A. quadrimaculata* (Mahunka, 1988) from Malaysia (see Mahunka 1988), *A. rotundiceps* Aoki, 1996 from Japan and Vietnam (see Aoki 1996) and *A. plowmanae* Balogh & Balogh, 1983 from Australia (see Balogh and Balogh 1983) in having small body size, minute prodorsal setae, four pairs of rounded notogastral porose areas and bothridial setae with unilaterally dilated head. However, the new species differs from these species by having densely ciliate bothridial heads (versus slightly barbed in distal parts), larger body size (282–298 × 215–232 versus 243–264 × 193–202 in *A. borhidii*, 249 × 166<sup>2</sup> in *A. quadrimaculata*, 212–219 × 155–160 in *A. rotundiceps* and 261 × 171 in *A. plowmanae*) and absence of a median pore (versus present in *A. borhidii*, *A. quadrimaculata* and *A. rotundiceps*).

***Allogalumna paranovazealandica* sp. n.**

<http://zoobank.org/5DB5344A-F409-47AF-AF3A-EBDBADD7F990>

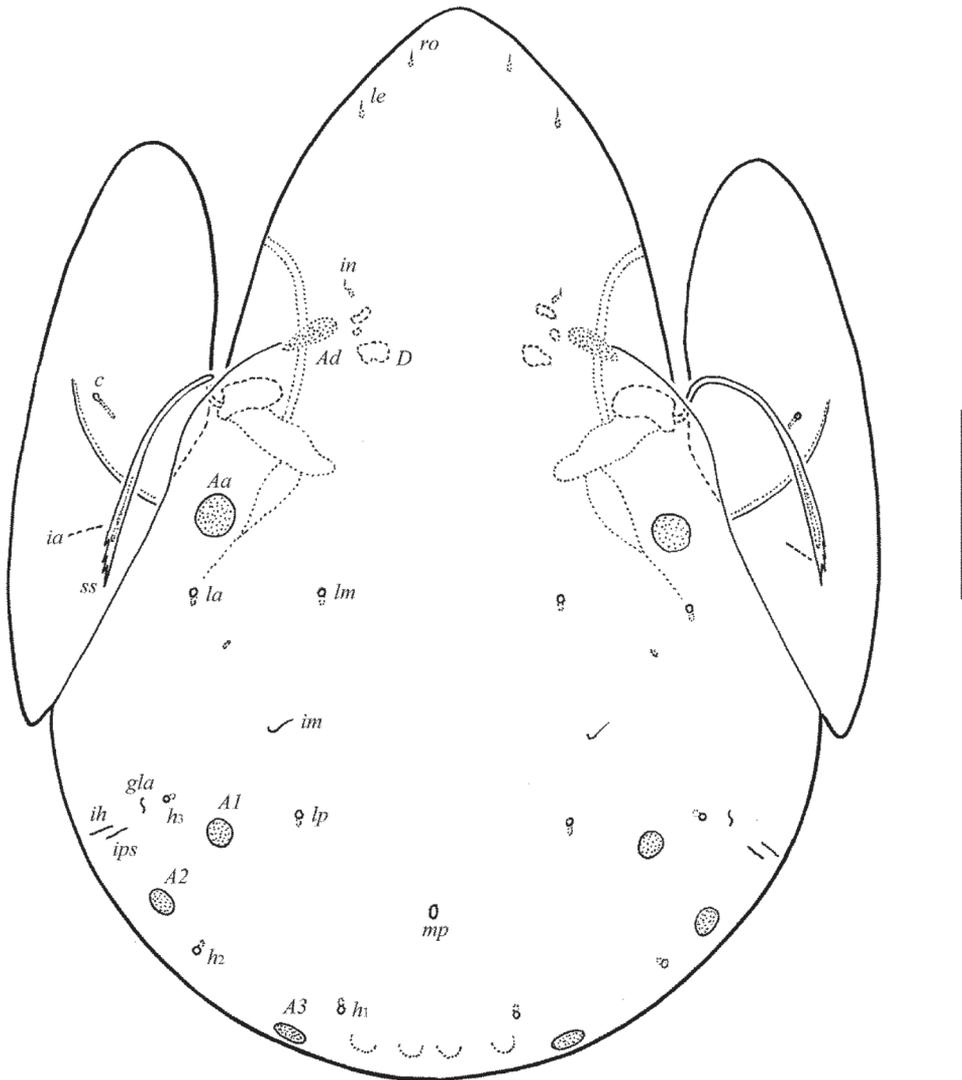
Figs 10–18

**Diagnosis.** Body size: 282–298 × 199–215. Rostral, lamellar and interlamellar setae minute. Bothridial setae with unilaterally slightly dilated, elongated, barbed in medio-distal part head. Anterior notogastral margin not developed. Four pairs of porose areas rounded. Median pore present. Postanal porose area elongate oval.

**Description.** *Measurements.* Body length: 282 (holotype: female), 282–298 (seven paratypes: two females and five males); notogaster width: 215 (holotype), 199–215 (seven paratypes). Without sexual dimorphism.

*Integument.* Body color brown. Body surface, pteromorphs, subcapitular mentum, genital and anal plates, and legs smooth.

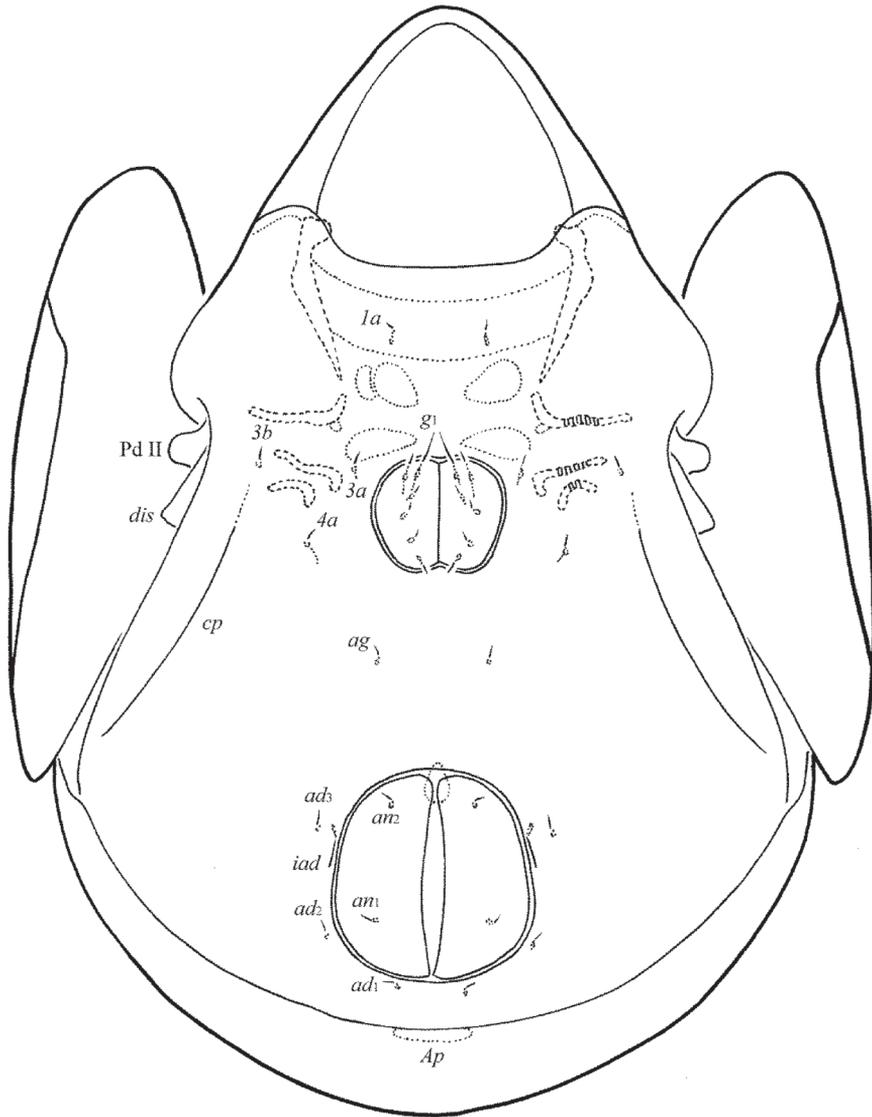
<sup>2</sup> Mahunka (1988) presented the following body size for *A. quadrimaculata* (systematic placement for this species in *Allogalumna* established by Ermilov and Bayartogtokh 2015): 389–405 × 275–300. We studied the sizes of two paratypes of *P. quadrimaculata*, and found 249 × 166. Hence, this corrected data could be used in future identification of *A. quadrimaculata*.



**Figure 10.** *Allogalumna paranovazealandica* sp. n., adult: dorsal view. Scale bar 50  $\mu$ m.

*Prodorsum* (Figs 10, 12, 14). Rostrum broadly rounded. Sublamellar lines distinct, curving backwards. Rostral, lamellar and interlamellar setae minute (all 4), thin, smooth. Bothridial setae long (77–86), with unilaterally slightly dilated, elongated, barbed in medio-distal part head, directed postero-laterad. Exobothridial setae and their alveoli absent. Porose areas *Ad* elongate oval, transversally oriented (12–16  $\times$  6–8).

*Notogaster* (Figs 10, 12, 13). Anterior notogastral margin not developed. Dorsopragnata of medium size, elongated longitudinally. Notogastral setae represented by 10 pairs of alveoli. Four pairs of porose areas rounded, with distinct margins: *Aa* (14–16)



**Figure 11.** *Allogalumna paranovaezealandica* sp. n., adult: ventral view (gnathosoma and legs not shown). Scale bar 50  $\mu$ m.

larger than *A1*, *A2* and *A3* (all 6–10). Setal alveoli *la* inserted posteriorly to *Aa*. Median pore present in males and females, located between *A2*. All lyrifissures distinct, *im* located between setal alveoli *lm* and *lp*. Opisthonotal gland openings located laterally to *A1*.

*Gnathosoma* (Fig. 15). Morphology of subcapitulum, palps and chelicerae typical for most Galumnidae (for example, see Engelbrecht 1969, 1972; Ermilov and Anichkin 2010, 2011; Ermilov et al. 2011, 2013b; Bayartogtokh and Akrami 2014). Subcapitulum size: 73  $\times$  61–65. Subcapitular setae setiform, smooth, *a* (12) longer

than *m* (8) and *h* (4), *a* thickest, *h* thinnest. Two pairs of adoral setae (6–8) thin, indistinctly barbed. Palps (61) with typical setation: 0–2–1–3–9(+ $\omega$ ). Axillary sacculi (*sac*) distinct. Chelicerae (82) with two setiform, barbed setae; *cha* (28) longer than *chb* (16). Trägårdh's organ long, tapered.

*Epimeral and lateral podosomal regions* (Fig. 11). Anterior tectum of epimere I smooth. Apodemes 1, 2, sejugal and 3 well visible. Four pairs of short (all 4), thin setae, setal formula: 1–0–1–2. Pedotecta II scale-like in lateral view, rounded distally in ventral view. Discidia sharply triangular. Circumpedal carinae indistinctly developed, directed to setae *3b*.

*Anogenital region* (Figs 11, 13, 16, 17). Six pairs of genital ( $g_1$ , 10;  $g_2$ – $g_6$ , 4), one pair of aggenital (4), two pairs of anal (4) and three pairs of adanal (4) setae thin, smooth. Two genital setae on anterior edge of each genital plate. Adanal setae *ad*<sub>3</sub> inserted laterally to adanal lyrifissures. Postanal porose area elongate oval, transversally oriented (20 × 6–8).

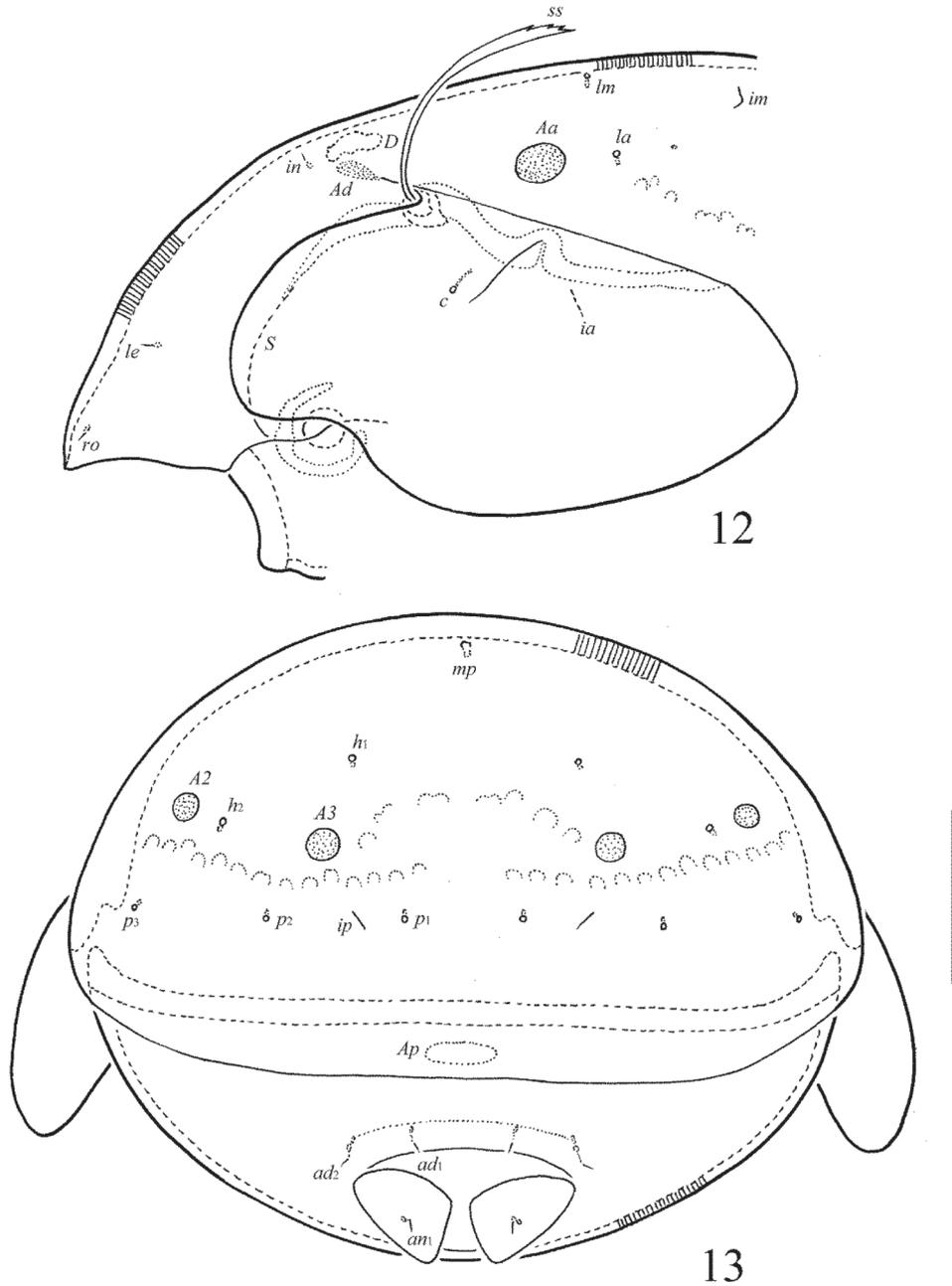
*Legs* (Fig. 18). Morphology of leg segments, setae and solenidia typical for most Galumnidae (for example, see Engelbrecht 1969, 1972; Ermilov and Anichkin 2010, 2011; Ermilov et al. 2011; Bayartogtokh and Akrami 2014). Tridactylous; claws smooth. Formulas of leg setation and solenidia: I (1–4–3–4–20) [1–2–2], II (1–4–3–4–15) [1–1–2], III (1–2–1–3–15) [1–1–0], IV (1–2–2–3–12) [0–1–0]; homology of setae and solenidia indicated in c Solenidion  $\psi$  of tibiae IV inserted dorsally at about 2/3 length of segment.

**Material examined.** Holotype (female): Indonesia, Sumatra, Bukit Duabelas landscape, Jungle rubber agroforest, research site BJ5, 02°08'35.6"S, E 102°51'04.7"E, 51 m a.s.l., from upper soil layer (0–5 cm). Four paratypes (female and three males): Indonesia, Sumatra, Harapan landscape, Rubber plantation, research site HR2, 01°52'44.5"S, 103°16'28.4"E, 59 m a.s.l., from upper soil layer (0–5 cm). Three paratypes (female and two males): Indonesia, Sumatra, Harapan landscape, secondary rainforest, research site HF4, S 02°11'15.2"S, 103°20'33.4"E, from upper soil layer (0–5 cm). All specimens were collected by Bernhard Klarner (15.XI.2013) and determined and collected to morphospecies level by Dorothee Sandmann.

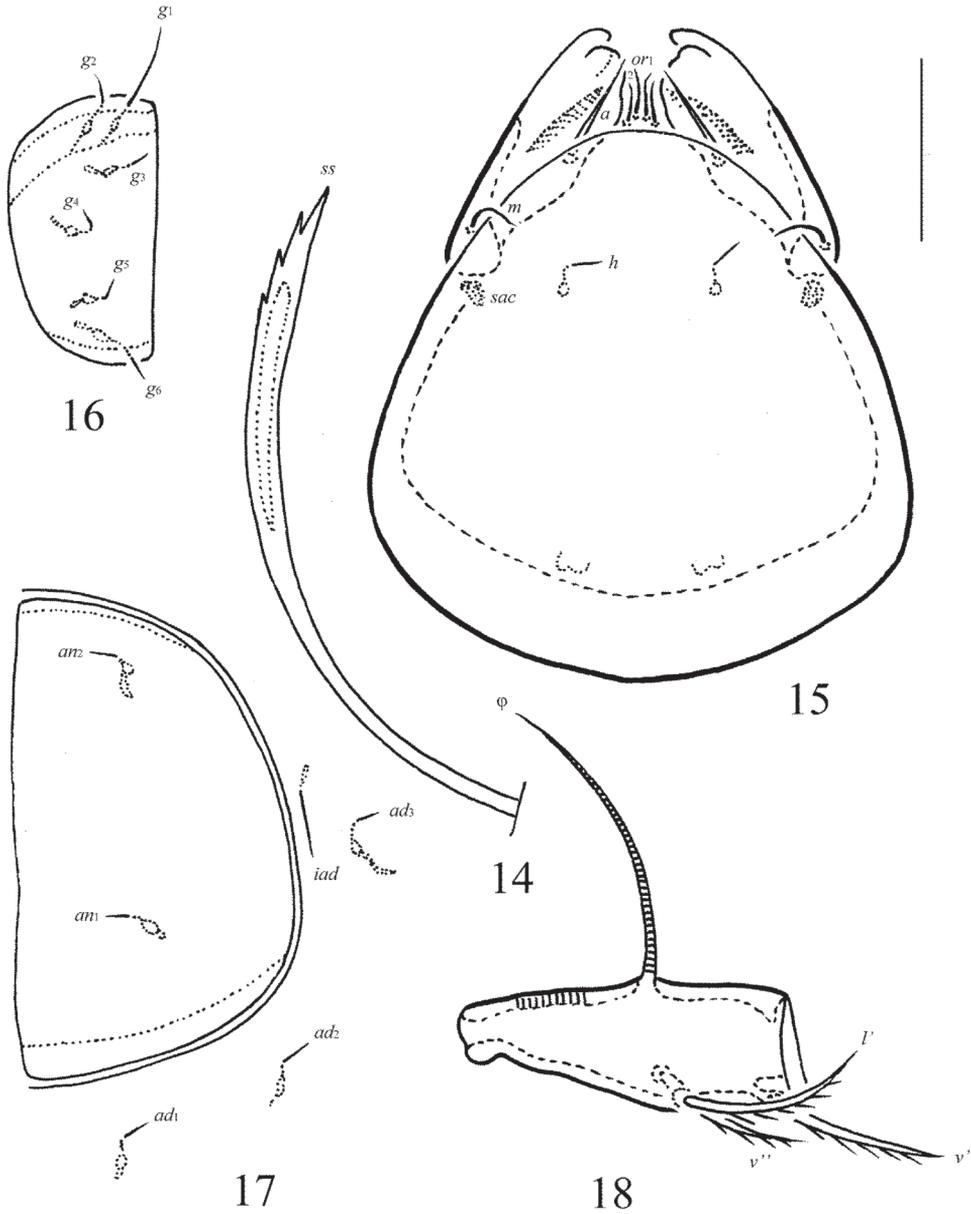
**Type deposition.** The holotype is deposited in LIPI (Indonesian Institute of Science) Cibinong, Indonesia; three paratypes are deposited in the collection of the Senckenberg Museum, Görlitz, Germany; four paratypes are deposited in the collection of the Tyumen State University Museum of Zoology, Tyumen, Russia.

**Etymology.** The specific name *paranovazealandica* refers to the morphological similarity of the new species to *Allogalumna novazealandica* Hammer, 1968.

**Remarks.** *Allogalumna paranovazealandica* sp. n. is most similar to *A. novazealandica* Hammer, 1968 from New Zealand in having minute prodorsal setae, long bothridial setae with slightly dilated head, four pairs of rounded notogastral porose areas, median pore and elongated postanal porose area. However, the new species differs from the latter by the shorter body length (282–298 versus 400–410 in *A. novazealandica*) and barbed in medio-distal part and curving postero-laterad bothridial setae (versus smooth and straight, directed upwards-laterally in *A. novazealandica*).



**Figures 12–13.** *Allogalumna paranovazealandica* sp. n., adult: **12** anterior part of body, lateral view (gnathosoma and leg I not shown) **13** posterior view. Scale bar 50  $\mu$ m.



**Figures 14–18.** *Allogalumna paranovaezealandica* sp. n., adult: **14** bothridial seta **15** subcapitulum, ventral view **16** genital plate, right **17** anal plate, left, and adanal setae **18** tibia of leg IV, left, antiaxial view. Scale bar 20  $\mu$ m.

## Acknowledgements

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# Contributions to the knowledge of oribatid mites of Indonesia. 2. The genus *Pergalumna* (Galumnidae) with description of a new species and key to known species in the Oriental region (Acari, Oribatida)

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## Abstract

A new species of oribatid mite of the genus *Pergalumna* (Oribatida, Galumnidae) is described from litter and soil materials in Sumatra, Indonesia. *Pergalumna paraindistincta* sp. n. is morphologically most similar to *P. indistincta* Ermilov & Anichkin, 2011, *P. pertrichosa* Mahunka, 1995 and *P. sura* Balogh, 1997; however, the new species differs from *P. indistincta* by the smaller body size, presence of long adanal setae  $ad_1$ , and large, single median pore in females and males; from *P. pertrichosa* by the smaller body size, presence of three pairs of notogastral porose areas, elongated *AI* and minute anal setae; from *P. sura* by the presence of strong adanal setae  $ad_1$ , large, single median pore in females and males, and shorter bothridial setae. Furthermore, *Pergalumna hawaiiensis hawaiiensis* (Jacot, 1934) and *P. panayensis* Ermilov & Corpuz-Raros, 2015 are recorded for the first time in the Indonesian fauna. An identification key to the known species of *Pergalumna* in the Oriental region is given.

## Keywords

Oribatid mites, *Pergalumna*, new species, new record, key, Indonesia, Oriental region

## Introduction

This work is a part of a continuing study on the Indonesian fauna of oribatid mites, and it includes the data on the genus *Pergalumna* Grandjean, 1936 (Oribatida, Galumnidae). During taxonomic identification, four species were identified, including one new to science. The primary goal of the paper is to present data on the specific localities, notes on new records and overall known distributions of registered taxa and to describe the new species.

*Pergalumna* is a genus that was proposed by Grandjean (1936) with *Oribata nervosa* Berlese, 1914 as type species. Based on an updated generic diagnosis (Ermilov et al. 2013b), it comprises more than 140 species (Subías 2004, updated 2015; Ermilov and Bayartogtokh 2015; Ermilov and Corpuz-Raros 2015) having collectively a cosmopolitan distribution (Subías 2004, updated 2015). The identification keys to selected species were given by Shaldybina (1975), Balogh and Balogh (1990, 2002), Weigmann (2006), and Ermilov et al. (2014b). The secondary goal of the paper is to provide an identification key to known species of *Pergalumna* in the Oriental region.

## Materials and methods

Exact collection locality and habitat are given in the respective “Material examined” section for each species.

Specimens were mounted in lactic acid on temporary cavity slides for measurement and illustration. The body length was measured in lateral view, from the tip of the rostrum to the posterior edge of the ventral plate. Notogastral width refers to the maximum width in dorsal aspect. Lengths of body setae were measured in lateral aspect. All body measurements are presented in micrometers. Formulas for leg setation are given in parentheses according to the sequence trochanter–femur– genu–tibia–tarsus (famulus included). Formulas for leg solenidia are given in square brackets according to the sequence genu–tibia–tarsus.

General terminology used in this paper follows that of Grandjean (summarized by Norton and Behan-Pelletier 2009).

Drawings were made with a camera lucida using a Carl Zeiss transmission light microscope “Axioskop-2 Plus”.

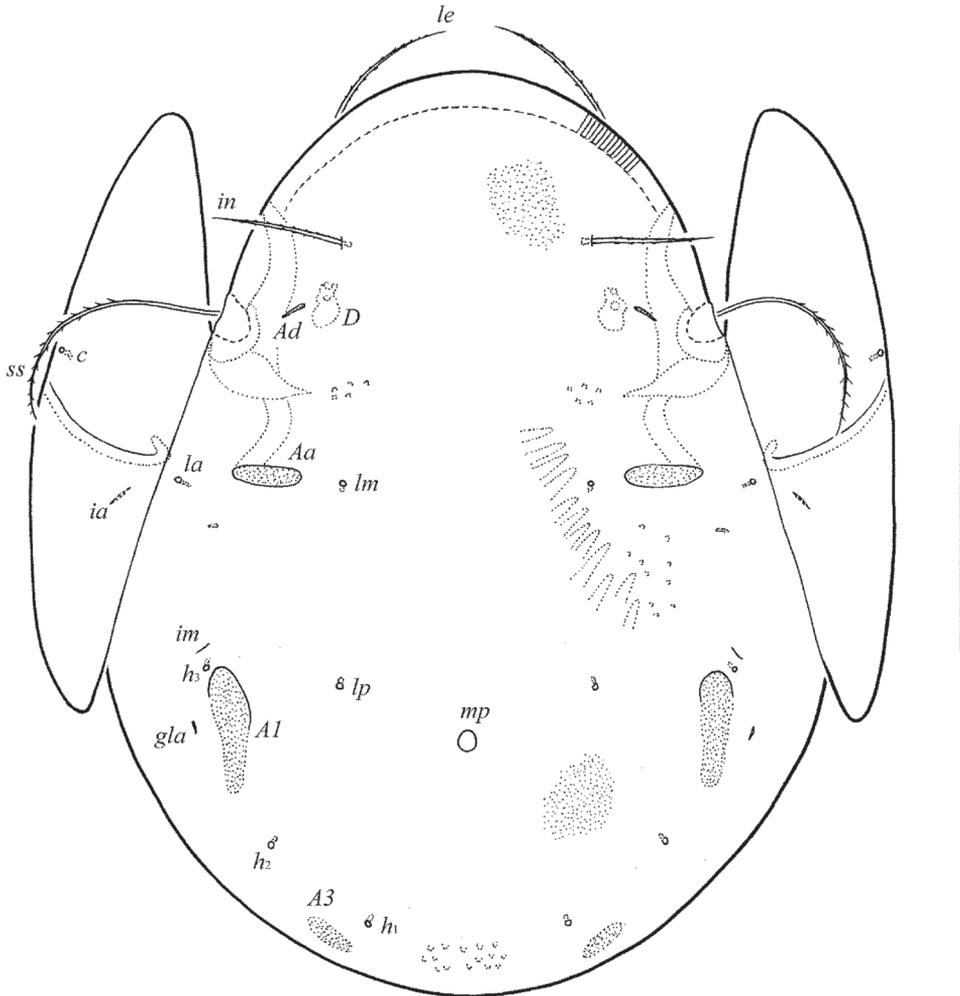
## Description

### *Pergalumna paraindistincta* sp. n.

<http://zoobank.org/F1F876B8-867F-4EA9-851D-FB4186C05342>

Figs 1–9

**Diagnosis.** Body size: 415–481 × 298–365. Rostral, lamellar and interlamellar setae well developed, barbed. Bothridial setae long, setiform, ciliate. Anterior notogastral



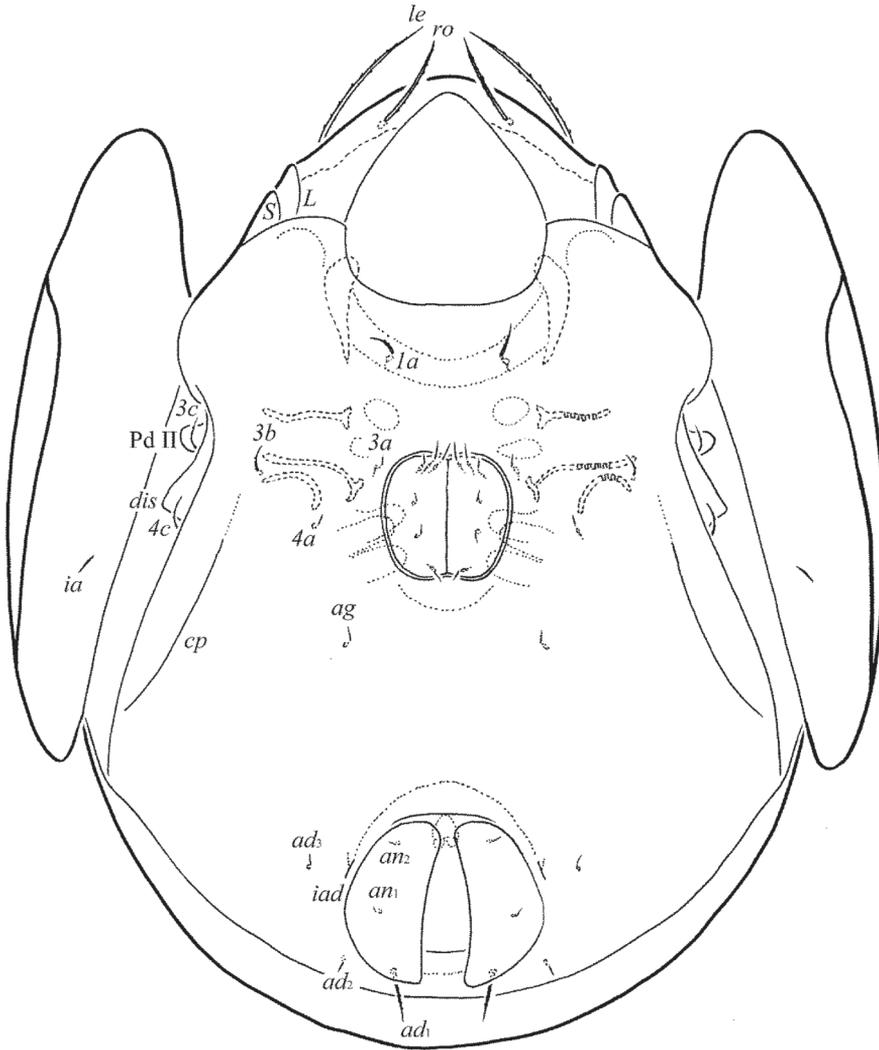
**Figure 1.** *Pergalumna paraindistincta* sp. n., adult: dorsal view. Scale bar 100  $\mu$ m.

margin not developed. Three pairs of elongate oval porose areas on notogaster, *Aa* transversally oriented, located between *la* and *lm*, *A1* longitudinally oriented. Median pore single, large. Adanal setae *ad*<sub>1</sub> of medium size, straight, heavily barbed. Postanal porose area absent.

**Description.** *Measurements.* Body length: 431 (holotype: male), 415–481 (10 paratypes: three females and seven males); notogaster width: 298 (holotype), 298–365 (10 paratypes). Without sexual dimorphism.

*Integument.* Body color brown. Body surface microgranulate, visible under high magnification,  $\times 1000$  (diameter of granules less than 1).

*Prodorsum* (Figs 1, 3, 5). Rostrum broadly rounded. Lamellar (*L*) and sublamellar (*S*) lines distinct, parallel, curving backwards. Rostral (*ro*, 41–49), lamellar (*le*, 69–77) and interlamellar (*in*, 86–90) setae setiform, barbed. Bothridial setae (*bs*, 114–127)



**Figure 2.** *Pergalumna paraindincta* sp. n., adult: ventral view (gnathosoma and legs not shown). Scale bar 100  $\mu$ m.

setiform, densely ciliate in medio-distal parts. Exobothridial setae and their alveoli absent. Porose areas *Ad* narrowly elongate oval, transversally oriented (16–20  $\times$  4).

*Notogaster* (Figs 1, 3, 4). Anterior notogastral margin not developed. Dorsophragmata (*D*) of medium size, elongated longitudinally. Notogastral setae represented by 10 pairs of alveoli. Three pairs of porose areas: *Aa* clearly bordered, elongate oval, transversally oriented (28–32  $\times$  8–12), *Al* distinctly bordered only in anterior part, elongate oval to slightly elongate triangular, longitudinally oriented (57–68  $\times$  12–16), *A3* without clear borders, elongate oval (24–28  $\times$  8–12). Areas *Aa* located between setal alveoli

*la* and *lm*, equal distanced from them. Median pore present in males and females, comparatively large (diameter 10–16). All lyrifissures (*ia*, *im*, *ip*, *ih*, *ips*) distinct, *im* located antero-laterally to *A1*. Opisthonotal gland openings (*gla*) located laterally to *A1*.

*Gnathosoma* (Fig. 6). Morphology of subcapitulum, palps and chelicerae typical for *Pergalumna* (see Engelbrecht 1972; Ermilov and Anichkin 2011a, b). Subcapitulum size: 102–106 × 102–106. Subcapitular setae setiform, slightly barbed, *m* (14–16) shorter than *a* and *b* (both pairs 18–20); *a* thickest, *m* thinnest. Two pairs of adoral setae (*or*<sub>1</sub>, *or*<sub>2</sub>, 12–14) setiform, hook-like distally, barbed. Palps (90–94) with typical setation: 0–2–1–3–9(+ω). Axillary sacculi (*sac*) distinct. Chelicerae (164) with two setiform, barbed setae; *cha* (41) longer than *chb* (24). Trägårdh's organ long, tapered.

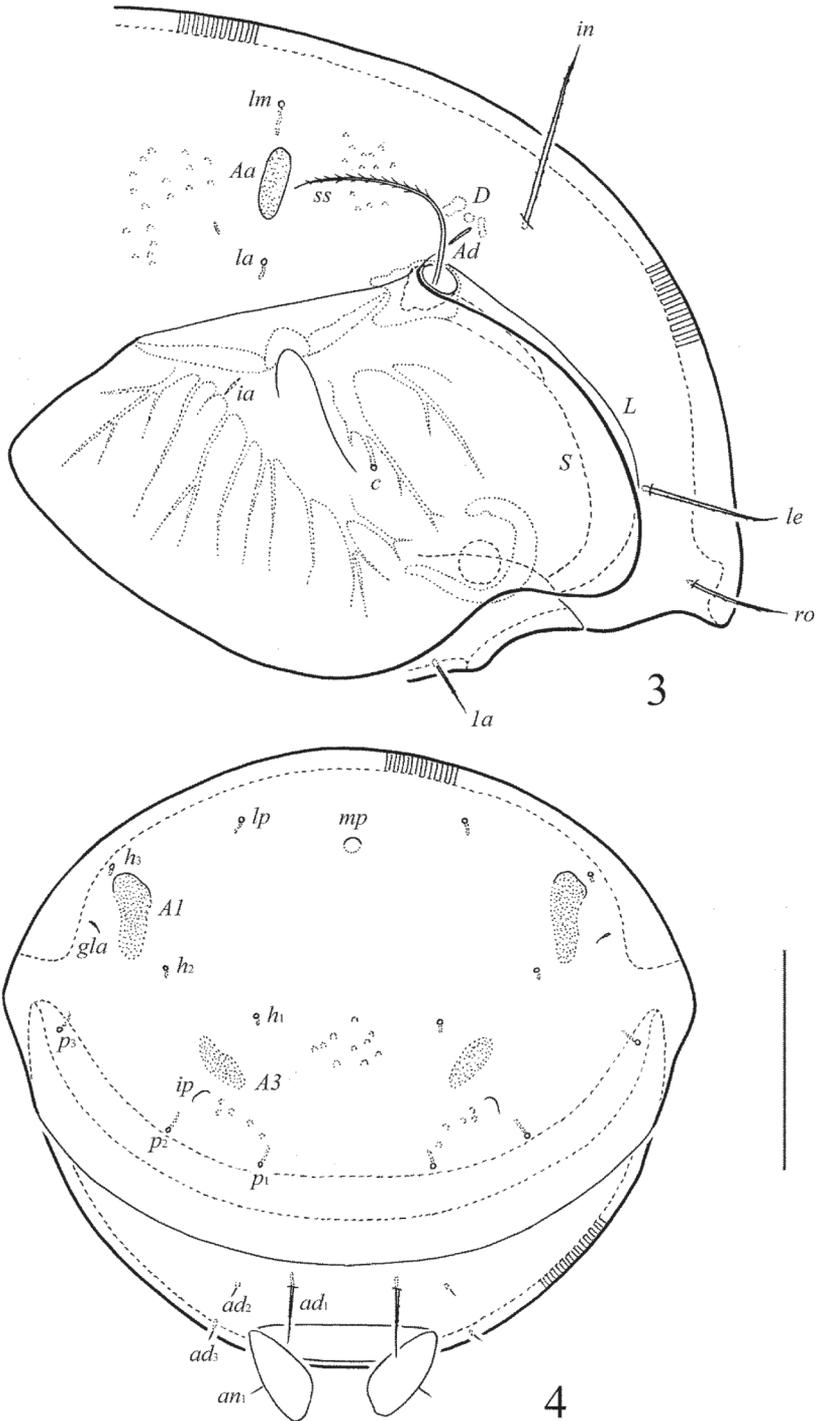
*Epimeral and lateral podosomal regions* (Fig. 2). Anterior tectum of epimere I smooth. Apodemes 1, 2, sejugal and 3 well visible. Six pairs of setae, setal formula: 1–0–2–3. Setae thin, slightly barbed, *1a*, *3c* and *4c* (24) longer than *3b* (10–14) and *4a* and *4b* (4); *1a* thicker than others. Pedotecta II (Pd II) scale-like in lateral view, rounded distally in ventral view. Discidia (*dis*) sharply triangular. Circumpedial carinae (*cp*) slightly developed.

*Anogenital region* (Figs 2, 4, 7, 8). Six pairs of genital (*g*<sub>1</sub>, *g*<sub>2</sub>, 12; *g*<sub>2</sub>–*g*<sub>6</sub>, 8), one pair of aggenital (*ag*, 8), two pairs of anal (*an*<sub>1</sub>, *an*<sub>2</sub>, 8) and two pairs of adanal setae (*ad*<sub>2</sub>, *ad*<sub>3</sub>, 8) thin, indistinctly barbed. One pair of adanal setae (*ad*<sub>1</sub>, 24–36) thickened, straight, heavily barbed, however, in three paratypes one seta of the *ad*<sub>1</sub> pair is short, as *ad*<sub>2</sub> and *ad*<sub>3</sub> in morphology. Adanal setae *ad*<sub>3</sub> inserted laterally to adanal lyrifissures (*iad*). Genital plates with two or three setae on anterior edge of each plate. Postanal porose area absent.

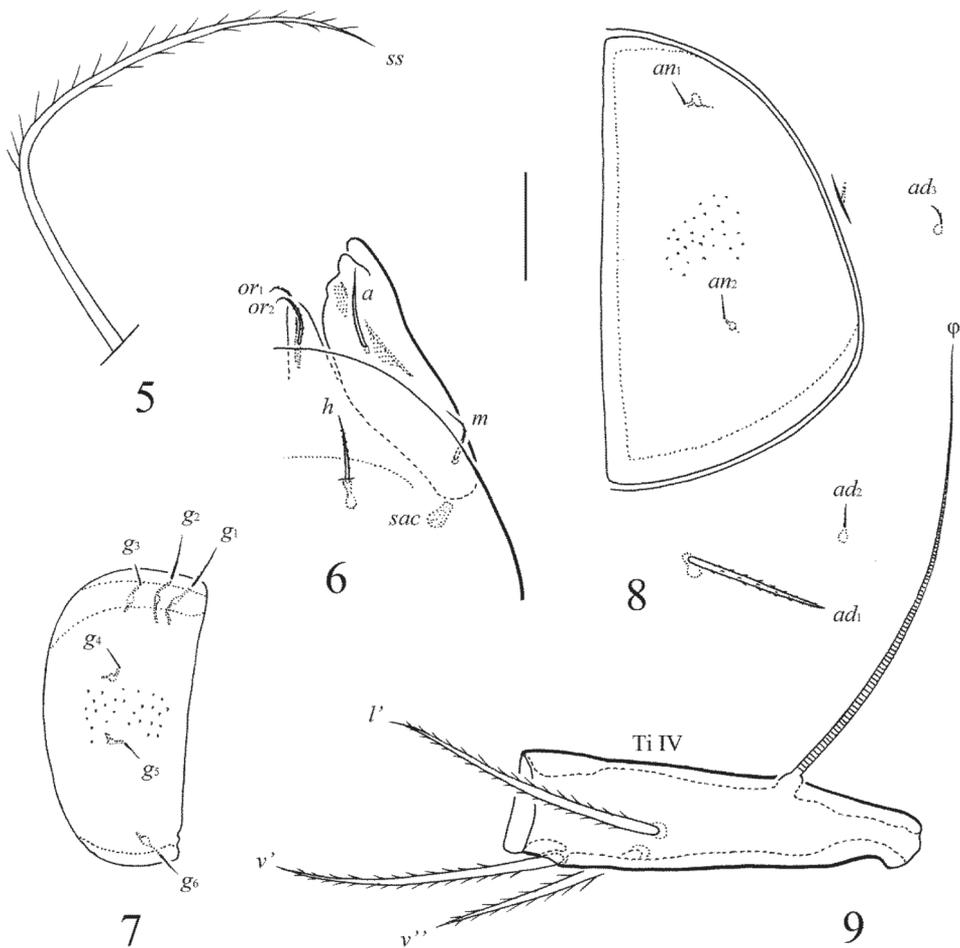
*Legs* (Fig. 9). Morphology of leg segments, setae and solenidia typical for *Pergalumna* (see Engelbrecht 1972; Ermilov and Anichkin 2011a, b). Claws smooth. Formulas of leg setation and solenidia: I (1–4–3–4–20) [1–2–2], II (1–4–3–4–15) [1–1–2], III (1–2–1–3–15) [1–1–0], IV (1–2–2–3–12) [0–1–0]; homology of setae and solenidia indicated in Table 1. Solenidion  $\psi$  of tibiae IV inserted dorsally in posterior part of segments.

**Material examined.** Holotype (male): Indonesia, Sumatra, Harapan landscape, secondary rainforest, research site HF1, 02°09'09.9"S, 103°21'43.2"E, 76 m a.s.l., from forest floor litter material. Six paratypes (two females and four males): Indonesia, Sumatra, Harapan landscape, rubber plantation, research site HR2, 01°52'44.5"S, 103°16'28.4"E, 59 m a.s.l., from forest floor litter material. Four paratypes (one female and three males): Sumatra, Indonesia, Harapan landscape, jungle rubber agroforest, research site HJ1, 01°55'40.0"S, 103°15'33.8"E, 51 m a.s.l., from forest floor litter material. All specimens were collected by Bernhard Klarner (15.XI.2013) and identified and collected to morphospecies level by Dorothee Sandmann.

**Type deposition.** The holotype is deposited in LIPI (Indonesian Institute of Science) Cibinong, Indonesia; three paratypes are in the collection of the Senckenberg Museum, Görlitz, Germany; seven paratypes are in the collection of the Tyumen State University Museum of Zoology, Tyumen, Russia.



**Figures 3–4.** *Pergalumna paraindistincta* sp. n., adult: **3** anterior part of body, lateral view (gnathosoma and leg I not shown) **4** posterior view. Scale bar 100  $\mu$ m.



**Figures 5–9.** *Pergalumna paraindistincta* sp. n., adult: **5** bothridial seta **6** anterior part of left half of subcapitulum, ventral view **7** genital plate, right **8** anal plate, left, and adanal setae **9** tibia of leg IV, right, antiaxial view. Scale bar 20  $\mu$ m.

**Table I.** Leg setation and solenidia of adult *Pergalumna paraindistincta* sp. n.

Leg	Tr	Fe	Ge	Ti	Ta
I	$v'$	$d, (l), bv''$	$(l), v', \sigma$	$(l), (v), \varphi_1, \varphi_2$	$(ft), (tc), (it), (p), (u), (a), s, (pv), v', (pl), l'', \varepsilon, \omega_1, \omega_2$
II	$v'$	$d, (l), bv''$	$(l), v', \sigma$	$(l), (v), \varphi$	$(ft), (tc), (it), (p), (u), (a), s, (pv), \omega_1, \omega_2$
III	$v'$	$d, ev'$	$l', \sigma$	$l', (v), \varphi$	$(ft), (tc), (it), (p), (u), (a), s, (pv)$
IV	$v'$	$d, ev'$	$d, l'$	$l', (v), \varphi$	$ft'', (tc), (p), (u), (a), s, (pv)$

Note: Roman letters refer to normal setae, Greek letters to solenidia (except  $\varepsilon$  = famulus). Single prime (') marks setae on the anterior and double prime (") setae on the posterior side of a given leg segment. Parentheses refer to a pair of setae. Tr – trochanter, Fe – femur, Ge – genu, Ti – Tibia, Ta – tarsus.

**Etymology.** The specific name *paraindistincta* refers to the morphological similarity of the new species to *Pergalumna indistincta* Ermilov & Anichkin, 2011.

**Remarks.** *Pergalumna paraindistincta* sp. n. is morphologically most similar to *P. indistincta* Ermilov & Anichkin, 2011 from Vietnam (see Ermilov and Anichkin 2011b) and *P. sura* Balogh, 1997 from the Neotropical region (see Balogh 1997; Ermilov et al. 2014a) in having rounded rostrum, well-developed prodorsal setae, setiform and ciliate of bothridial setae, three pairs of notogastral porose areas, transversally oriented *Aa* and strongly elongated, longitudinally oriented *AI*, and the absence of anterior notogastral margin as well as postanal porose area. However, the new species differs from both by the presence of strong adanal setae *ad*<sub>1</sub> (vs. minute in *P. indistincta* and *P. sura*) and large, single median pore in females and males (vs. median pore absent in males and represented by several foveae in females in *P. indistincta*, and absent in females and males in *P. sura*). Additionally, the new species is smaller than *P. indistincta* (415–481 × 298–365 vs. 547–614 × 381–415) and has shorter bothridial setae than *P. sura*.

Furthermore, *P. paraindistincta* sp. n. is morphologically similar to *P. pertrichosa* Mahunka, 1995 from Borneo (see Mahunka 1995) in having a rounded rostrum, well developed prodorsal setae, setiform and ciliate bothridial setae, strong adanal setae *ad*<sub>1</sub>, a single median pore, and the absence of an anterior notogastral margin. However, the new species differs from the latter by the smaller body size (415–481 × 298–365 vs. 550–608 × 413–454 in *P. pertrichosa*), presence of three pairs of notogastral porose areas with elongated *AI* (vs. four pairs of porose areas with *AI* rounded in *P. pertrichosa*) and minute anal setae (vs. well developed in *P. pertrichosa*).

## Records

*Pergalumna hawaiiensis hawaiiensis* (Jacot, 1934) (see Jacot 1934a). Distribution: Pacific Islands. New record for Indonesia.

**Material examined.** One specimen: Indonesia, Sumatra, Harapan landscape, Jungle rubber agroforest, research site HJ1, 01°55'40.0"S, 103°15'33.8"E, 51 m a.s.l., from upper soil layer (0–5 cm), 15.XI.2013 (B. Klarner). Three specimens: Indonesia, Sumatra, Bukit Duabelas landscape, rubber plantation, research site BR2, 02°05'06.8"S, 102°47'20.7"E, 95 m a.s.l., from upper soil layer (0–5 cm), 15.XI.2013 (B. Klarner). One specimen: Indonesia, Sumatra, Bukit Duabelas landscape, oil palm plantation, research site BO3, 02°04'15.2"S, 102°47'30.6"E, 71 m a.s.l., from upper soil layer (0–5 cm), 15.XI.2013 (B. Klarner).

*Pergalumna panayensis* Ermilov & Corpuz-Raros, 2015 (see Ermilov and Corpuz-Raros 2015). Distribution: Philippines. New record for Indonesia.

**Material examined.** One specimen: Indonesia, Sumatra, Harapan landscape, rubber plantation, research site HR2, 01°52'44.5"S, 103°16'28.4"E, 59 m a.s.l., from forest

floor litter material, 15.XI.2013 (B. Klarner). One specimen: same data, but in upper soil layer (0–5 cm). One specimen: Indonesia, Sumatra, Bukit Duabelas landscape, jungle rubber agroforest, research site BJ4, 02°00'57.3"S, 102°45'12.3"E, 60 m a.s.l., from upper soil layer (0–5 cm), 15.XI.2013 (B. Klarner).

*Pergalumna pterinervis* (Canestrini, 1898) (see Mahunka 1992). Distribution: Oriental region. New record for Indonesia.

**Material examined.** One specimen: Indonesia, Sumatra, Harapan landscape, jungle rubber agroforest, research site HJ2, 01°49'31.9'S, 103°17'39.2"E, 84 m a.s.l., from forest floor litter material, 15.XI.2013 (B. Klarner). One specimen: Indonesia, Sumatra, Harapan landscape, jungle rubber, research site HJ4, 01°47'07.3"S, 103°16'36.9"E, 57 m a.s.l., from upper soil layer (0–5 cm), 15.XI.2013 (B. Klarner). One specimen: Indonesia, Sumatra, Bukit Duabelas landscape, secondary rainforest, research site BF2, 01°58'55.1"S, 102°45'02.7"E, 77 m a.s.l., from upper soil layer (0–5 cm), 15.11.2013 (B. Klarner). Three specimens: Indonesia, Sumatra, Harapan landscape, jungle rubber agroforest, research site HJ2, 01°49'31.9"S, 03°17'39.2"E, 84 m a.s.l., from forest floor litter material, 15.XI.2013 (B. Klarner).

### Key to known species of *Pergalumna* in the Oriental region

At present, 45 species/subspecies of *Pergalumna* are known in the Oriental region (Subías 2004, updated 2015; including present and personal data of the first author).

*Pergalumna heroica* (Willmann, 1931) from Java (see Willmann 1931), *P. medialis* (Sellnick, 1925) from Sumatra (see Sellnick 1925) and *P. obsessa* Subías, 2004 from Taiwan (see Tseng 1984 as *Galumna pallida* Tseng, 1984) are excluded from the key because these species have been poorly described.

*Pergalumna curva curva* (Ewing, 1907) from the Holarctic and Oriental regions (see Ewing 1907; Jacot 1934b), *P. curva ventralis* (Willmann, 1931) from the Holarctic, Neotropical and Oriental regions and Polynesia (see Willmann 1931; Jacot 1934b; Hammer 1958, 1961, 1972), *P. obvia obvia* (Berlese, 1914) from the Ethiopian, Neotropical, Oriental and Palaearctic regions, and Hawaii and U.S.A. (see Weigmann 2006; Ermilov et al. 2013c), *P. operata* Tseng, 1984 from Taiwan (see Tseng 1984) and *P. pyramidalis* (Tseng, 1984) from Taiwan (see Tseng 1984) were not included because systematic placement of these species is not clear. We consider *P. obvia obvia* as a representative of the genus *Galumna* Heyden, 1826 (see Ermilov et al. 2013c). *Pergalumna curva curva*, *P. curva ventralis* and *P. operata* Tseng, 1984 have distinct notogastral setae, which are not traits for *Pergalumna* (see generic diagnosis in Ermilov et al. 2013b); these species are poorly described and redescribed; however, based on available data they should be considered as representatives of the genus *Allogalumna* Grandjean, 1936 or *Trichogalumna* Balogh, 1960 (depending on presence or absence of lamellar lines). *Pergalumna pyrami-*

*dalis* has 14 pairs of notogastral setal alveoli, developed lamellae directed to insertions of lamellar setae and pteromorphs without setae (Tseng 1984); most likely this species is a representative of the subgenus *Neoribates* (*Neoribates*) Berlese, 1914 (Oripodoidea, Parakalummidae), and it is morphologically most similar to *N. (N.) paratuberculatus* Ermilov, Shtanchaeva & Subías, 2014 from Vietnam (see Ermilov et al. 2014d) and *N. (N.) tuberculatus* Willmann, 1956 from “Czechoslovakia” (see Willmann 1956) in having tubercles on pteromorphs and some other characters.

- 1 Anterior margin of notogaster of specific structure, tuberculate ..... **2**
- Anterior margin of notogaster simple, smooth or not developed ..... **3**
- 2 Genital plates with several striae; notogastral porose areas of medium size, larger than diameter of bothridia; body size: 451–490 × 328–366.....
- ....***P. margaritata* Mahunka, 1989 (Mahunka 1989)**. Distribution: Vietnam
- Genital plates with one pair of striae; notogastral porose areas small, similar to diameter of bothridia; body size: 402–447 × 281–315..... ***P. pseudomargaritata* Mahunka, 1994** (see Mahunka 1994). Distribution: Thailand
- 3 Anterior margin of notogaster distinctly developed, complete..... **4**
- Anterior margin of notogaster not developed ..... **12**
- 4 Rostrum pointed ..... **5**
- Rostrum rounded ..... **7**
- 5 Four pairs of notogastral porose areas; *Aa* elongate triangular, transversally oriented; lateral parts of pteromorphs with strong ridges forming slightly visible reticulate pattern; body size: 517–670 × 397–525.....
- ....***P. altera* (Oudemans, 1915)** (see Aoki 1961 as *P. harunaensis* Aoki 1961, 1975; Engelbrecht 1972; Weigmann 2006). Distribution: Semicosmopolitan
- Three pairs of notogastral porose areas; *Aa* rounded; pteromorphs without strong ridges and reticulate pattern ..... **6**
- 6 Interlamellar setae long; posterior part of notogaster without furrows; body size: 664–830 × 498–630..... ***P. jurtaevi* Ermilov & Anichkin, 2011** (see Ermilov and Anichkin 2011a; Ermilov et al. 2012a). Distribution: Vietnam
- Interlamellar setae represented by alveoli; posterior part of notogaster with two parallel, longitudinal furrows; body size: 664–830 × 498–630 .....
- .....***P. asetosa* Ermilov, Shtanchaeva, Kalúz & Subías, 2013** (see Ermilov et al. 2013a). Distribution: India
- 7 Bothridial setae setiform; body size: 520–676 × 502.....
- ..... ***P. foveolata* Hammer, 1973** (see Hammer 1973; Bayartogtokh and Chatterjee 2010). Distribution: Australian, Neotropical and Oriental region
- Bothridial setae with developed head ..... **8**
- 8 Interlamellar setae minute; body surface foveolate; body size: 222–235 × 177–190.....
- ....***P. annulata* Mahunka, 1995** (see Mahunka 1995). Distribution: Borneo
- Interlamellar setae long; body surface not foveolate..... **9**

- 9 Three pairs of notogastral porose areas; *Aa* rounded; body length: 820..... ***P. corniculata* (Berlese, 1905)** (see Berlese 1905; Mahunka 1992). Distribution: Java
- Four pairs of notogastral porose areas; *Aa* elongated, transversally oriented ... **10**
- 10 Notogastral porose areas *Aa* triangular; median pore present; body size: 623 × 533 ..... ***P. taprobanica* Balogh, 1988** (see Balogh 1988). Distribution: Oriental region
- Notogastral porose areas *Aa* elongate oval to boot-shaped..... **11**
- 11 Bothridial setae fusiform, with well-developed head rounded distally; postanal porose area present; body size: 672 × 528..... ***P. andbraense* Raju, Appalanaidu & Rao, 1981** (see Raju et al. 1981). Distribution: India
- Bothridial setae lanceolate, with slightly developed head pointed distally; postanal porose area absent; body size: 830–898 × 630–680 ..... ***P. paraelongata* Ermilov & Anichkin, 2012** (see Ermilov et al. 2012b). Distribution: Vietnam
- 12 Rostrum trapezoid; anal setae comparatively long, longer than width of anal plate; body size: 1278–1311 × 976–1045..... ***P. paraclericata* Ermilov, Chatterjee, Das & Bordoloi, 2014** (see Ermilov et al. 2014c). Distribution: India
- Rostrum not trapezoid; anal setae comparatively short, shorter than width of anal plate ..... **13**
- 13 Rostrum pointed ..... **14**
- Rostrum rounded ..... **18**
- 14 Four pairs of notogastral porose areas; *Aa* located nearer to setal alveoli *la* than *lm*; body size: 730–780 × 564–597 ..... ***P. cattienica* Ermilov & Anichkin, 2011** (see Ermilov and Anichkin 2011a). Distribution: Vietnam
- Three pairs of notogastral porose areas; *Aa* located nearer to setal alveoli *lm* or distanced equal from *la* and *lm* ..... **15**
- 15 Interlamellar setae represented by alveoli; anterior part of prodorsum with two longitudinal ridges; notogastral porose areas *Aa* located nearer to setal alveoli *lm* than *la*; body size: 1162–1278 × 898–1012 ..... ***P. minipora* Ermilov, Chatterjee, Das & Bordoloi, 2014** (see Ermilov et al. 2014c). Distribution: India
- Interlamellar setae of medium size or long; prodorsum without ridges; notogastral porose areas *Aa* distanced equal from *la* and *lm*..... **16**
- 16 Notogastral porose areas *A1* elongated, longitudinally oriented; body surface foveolate; genital plates not striate; body size: 365–415 × 265–332 ..... ***P. paratsurusakii* Ermilov, Shtanchaeva, Kalúz & Subías, 2013** (see Ermilov et al. 2013a). Distribution: India
- Notogastral porose areas *A1* rounded; body surface not foveolate; genital plates striate ..... **17**
- 17 Adanal setae *ad*<sub>1</sub> and *ad*<sub>2</sub> comparatively long, not shorter than width of anal plate; median pore absent; interlamellar setae longer than bothridial setae; body size: 597–680 × 431–498..... ***P. paracattienica* Ermilov, Chatterjee, Das & Bordoloi, 2014** (see Ermilov et al. 2014c). Distribution: India

- Adanal setae  $ad_1$  and  $ad_2$  minute; median pore present; interlamellar setae shorter than bothridial setae; body size: 498–531 × 381–398 ..... ***P. mahunkai* Ermilov, Shtanchaeva, Kalúz & Subías, 2013** (see Ermilov et al. 2013a). Distribution: India
- 18 Four pairs of notogastral porose areas ..... **19**
- Three pairs of notogastral porose areas ..... **22**
- 19 Interlamellar setae represented by alveoli; notogastral porose areas *Aa* located anteriorly to setal alveoli *la*; body length: 730 ..... ***P. corolevuensis* Hammer, 1973** (see Hammer 1973). Distribution: Fiji and India
- Interlamellar setae of medium size or long; notogastral porose areas *Aa* located between setal alveoli *la* and *lm* ..... **20**
- 20 Notogastral porose areas *A1* located antero-medially to *A2*; interlamellar setae of medium size; body size: 745–842 × 567–640 ..... ***P. hauseri* Mahunka, 1995** (see Mahunka 1995). Distribution: Borneo
- Notogastral porose areas *A1* located anteriorly to *A2*; interlamellar setae long ..... **21**
- 21 Adanal setae  $ad_1$  and  $ad_2$  similar in length; median pore absent; body size: 510–630 × 410–481 ..... ***P. pterinervis* (Canestrini, 1898)** (see Canestrini 1898; Berlese 1905, 1914; Mahunka 1992; including our data). Distribution: Oriental region
- Adanal setae  $ad_1$  longer than  $ad_2$ ; median pore present; body size: 550–608 × 413–454 ..... ***P. pertrichosa* Mahunka, 1995** (see Mahunka 1995). Distribution: Borneo
- 22 Notogastral porose areas *Aa* located nearer to setal alveoli *la* than *lm*; bothridial setae clavate ..... **23**
- Notogastral porose areas *Aa* located nearer to setal alveoli *lm* than *la* or distanced equal from them; bothridial setae setiform or with slightly dilated, elongate head ..... **24**
- 23 Interlamellar setae minute, shorter than diameter of bothridia; body surface not foveolate; median pore represented by several foveae; body size: 262–282 × 192–209 ..... ***P. pseudosejugalis* Ermilov & Anichkin, 2012** (see Ermilov and Anichkin 2012). Distribution: Vietnam
- Interlamellar setae short, but longer than diameter of bothridia; body surface foveolate; median pore absent; body size: 246–275 × 186–212 ..... ***P. crassipora* Mahunka, 1995** (see Mahunka 1995). Distribution: Borneo
- 24 Notogastral porose areas *Aa* located nearer to setal alveoli *lm* than *la* ..... **25**
- Notogastral porose areas *Aa* distanced equal from *la* and *lm* ..... **30**
- 25 Notogastral porose areas minute, smaller than diameter of bothridia; body size: 527–612 × 390–428 ..... ***P. imadatei* Aoki & Hu, 1993** (see Aoki and Hu 1993). Distribution: Oriental region
- Notogastral porose areas well developed, larger than diameter of bothridia ... **26**

- 26 Body surface slightly striate; median pore represented by several foveae; body size: 610–715 × 475–545..... *Pergalumna hawaiiensis hawaiiensis* (Jacot, 1934) (see Jacot 1934a; including our data)
- Body surface not striate; median pore single or absent ..... 27
- 27 Interlamellar setae minute, shorter than diameter of bothridia; body length: 720..... *P. bimaculata* Hammer, 1973 (see Hammer 1973). Distribution: Polynesia and Philippines
- Interlamellar setae of medium size, longer than diameter of bothridia..... 28
- 28 Median pore present, large; body length: 720 ..... *P. remota* (Hammer, 1968) (see Hammer 1968). Distribution: New Zealand and India
- Median pore absent ..... 29
- 29 Bothridial setae densely ciliate; body size: 451–490 × 300–334 .....  
..... *P. kotschy* Mahunka, 1989 (see Mahunka 1989). Distribution: Vietnam
- Bothridial setae smooth; body size: 398–453 × 275–340 .....  
.... *P. indivisa* Mahunka, 1995 (see Mahunka 1995). Distribution: Borneo
- 30 Bothridial setae with slightly dilated, elongated head ..... 31
- Bothridial setae setiform ..... 33
- 31 Body surface heavily tuberculate; body size: 385–425 × 285–331 .....  
..... *P. granulata* Balogh & Mahunka, 1967 (see Balogh and Mahunka 1967). Distribution: Vietnam and Japan
- Body surface not tuberculate..... 32
- 32 Body surface heavily granulate; body size: 302–356 × 237–262 .....  
..... *P. punctulata* Balogh & Mahunka, 1967 (see Balogh and Mahunka 1967). Distribution: Vietnam
- Body surface smooth; body size: 437–465 × 310–324 .....  
..... *P. intermedia intermedia* Aoki, 1963 (see Aoki 1963, 1966). Distribution: Palaearctic and Oriental regions
- 33 Notogastral porose areas *A1* elongated, longitudinally oriented..... 34
- Notogastral porose areas *A1* rounded to oval ..... 36
- 34 Adanal setae *ad*<sub>1</sub> long, not shorter than width of anal plate; median pore single; body size: 415–481 × 298–365 .....  
..... *P. paraindistincta* sp. n. Distribution: Indonesia
- Adanal setae *ad*<sub>1</sub> minute; median pore absent or represented by several foveae.. 35
- 35 Postanal porose area absent; median pore present in females; body size: 547–614 × 381–415 ..... *P. indistincta* Ermilov & Anichkin, 2011 (see Ermilov and Anichkin 2011b). Distribution: Vietnam
- Postanal porose area present; median pore absent in females; body size: 576 × 426 ..... *P. magnipora capensis* Engelbrecht, 1972 (see Engelbrecht 1972). Distribution: Southern Africa and India
- 36 Body surface striate and short ridges; posterior part of notogaster with longitudinal concavity; body size: 408–485 × 298–352 ..... *P. menglunensis* Aoki & Hu, 1993 (see Aoki and Hu 1993). Distribution: southern China

- Body not striate and without short ridges; posterior part of notogaster without concavity ..... 37
- 37 Adanal setae  $ad_1$  and  $ad_2$  comparatively long, not shorter than width of anal plate; setae  $c$  developed on pteromorphs; body size: 514–597 × 365–431 ..... ***P. minutuberculata* Ermilov & Martens, 2014** (see Ermilov and Martens 2014). Distribution: Nepal
- Adanal setae  $ad_1$  and  $ad_2$  shorter than width of anal plate; setae  $c$  represented by alveoli on pteromorphs ..... 38
- 38 Interlamellar setae represented by alveoli; median pore present; body size: 863–1145 × 639–970 ..... ***P. panayensis* Ermilov & Corpuz-Raros, 2015** (see Ermilov and Corpuz-Raros 2015)
- Interlamellar setae of medium size or long; median pore absent ..... 39
- 39 Bothridial setae densely ciliate ..... 40
- Bothridial setae densely smooth ..... 41
- 40 Notogastral porose areas amorphous, without distinct borders; genital plates not striate; body size: 332–377 × 245–276 ..... ***P. amorpha* Mahunka, 2008** (see Mahunka 2008). Distribution: Thailand
- Notogastral porose areas with distinct borders; genital plates striate; body size: 390–435 × 282–315 ..... ***P. intermedia retroversa* Aoki & Hu, 1993** (see Aoki and Hu 1993). Distribution: southern China
- 41 Interlamellar setae comparatively short, about 1/3 as long as their mutual distance; genital plates smooth; body size: 742–845 × 589–653 ..... ***P. magnipora capillararis* Aoki, 1961** (see Aoki 1961). Distribution: Palaearctic and Oriental regions
- Interlamellar setae of medium size, about 1/2 as long as their mutual distance; genital plates striate; body size: 822–840 × 618–650 ..... ***P. magnipora xishuangbanna* Aoki & Hu, 1993** (see Aoki and Hu 1993). Distribution: southern China

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# Acoustic, genetic and morphological variations within the katydid *Gampsocleis sedakovii* (Orthoptera, Tettigoniodea)

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## Abstract

In an attempt to explain the variation within this species and clarify the subspecies classification, an analysis of the genetic, calling songs, and morphological variations within the species *Gampsocleis sedakovii* is presented from Inner Mongolia, China. Recordings were compared of the male calling songs and analysis performed of selected acoustic variables. This analysis is combined with sequencing of mtDNA - COI and examination of morphological traits to perform cluster analyses. The trees constructed from different datasets were structurally similar, bisecting the six geographical populations studied. Based on two large branches in the analysis, the species *Gampsocleis sedakovii* was partitioned into two subspecies, *Gampsocleis sedakovii sedakovii* (Fischer von Waldheim, 1846) and *Gampsocleis sedakovii obscura* (Walker, 1869). Comparing all the traits, the individual of Elunchun (ELC) was the intermediate type in this species according to the acoustic, genetic, and morphological characteristics. This study provides evidence for insect acoustic signal divergence and the process of subspeciation.

## Keywords

Acoustics, gene, morphology, subspecies, interim morphs

## Introduction

Acoustic signals are important in several social behaviors of insects, such as sexual selection (Derlink et al. 2014, Hirtenlehner and Römer 2014), predator defense (Kowalski et al. 2014), and species recognition (Marshall et al. 2008, Wikins et al. 2013). Most insects can make sounds using a variety of methods (Uvarov 1966). Members of the order Orthoptera, including katydids and crickets, utilize acoustic signals to communicate (Gray et al. 2014, Sarria et al. 2014). These signals, produced by the rubbing of a toothed vein on one wing against a plectrum on the other, results in songs by stridulation (Montealegre 2012, Robillard and Desutter-Grandcolas 2011).

*Gampsocleis* is a genus within Tettigoniidae, which includes sixteen species, eleven of which are found in China. *Gampsocleis sedakovii* (Fischer von Waldheim, 1846), a medium to large-sized, xerophilic, and slightly thermophilic katydid, is the most common and ubiquitous species distributed in northeast China. Individuals of *G. sedakovii* are generally classified into two subspecies, *Gampsocleis sedakovii sedakovii* (Fischer von Waldheim, 1846) and *Gampsocleis sedakovii obscura* (Walker, 1869), differing morphologically in body size and the proportions of forewings and the pronotum (Zhou et al 2011).

The individuals of both subspecies (*G. s. sedakovii* and *G. s. obscura*) are excellent singers, and males sing at any time throughout the day. The calling song of *G. s. sedakovii* was already reported in a previous study (Wu and Shi 2009), but the acoustic signals of *G. s. obscura* have not been documented in the literature. Similarly, no comparative analysis of the songs from the two groups has been attained, which encouraged the development of this work.

The ratio between forewing and pronotum of *G. s. sedakovii* is much higher than that of *G. s. obscura*, while the *G. s. obscura* looks stronger than *G. s. sedakovii*. An “interim form” was found, consisting of individuals which had an intermediate ratio of forewing and pronotum between the averages for *G. s. obscura* and *G. s. sedakovii*, raising the possibility that the division of the subspecies within *G. sedakovii* should be reconsidered (see also Rentz and Miller 1971).

Different insect species have different acoustic signals and these signals have been used as an invariable trait for the recognition of conspecifics and the discrimination of heterospecifics (Foster and Endler 1999). The interspecific specificity and intraspecific stability of insect songs are used as a significant index of classification (Montealegre-Z and Morris 2004, Hemp and Kehl 2010), although it remains difficult to distinguish cryptic species and subspecies. Sometimes the classification criteria for closely related species is unclear. Despite some molecular studies on *G. sedakovii*, the relationship between these two subspecies and a clear basis of classification has remained controversial. Therefore, new methods to clarify these two subspecies and classify the interim morphs are required.

Wing polymorphism is common in insects, such as katydids (Wang 2011), grasshoppers (Steenman et al. 2015), rice planthoppers (Liang et al 2015), and so on. Three types of polymorphism are recognized: species with separate macropterous and brachypterous forms, continuous wing forms, and continuous wing form but with

slightly reduced wing in the brachypterous form (Roháček 2012). The individuals of *G. sedakovii* have continuous wings, and wing morph was often considered as a classification basis. Therefore, the wing types of *G. sedakovii* were also examined to evaluate the differentiation of *G. sedakovii* and its subspecies.

In this study the differentiation of the individuals collected from six locations of Inner Mongolia were analyzed and compared. Acoustic, morphological, and genetic differences were examined carefully. The analysis of the variation in the acoustic structure of *G. sedakovii* from different geographical localities provided the basis for further explorations on the divergence on acoustic communication of this species and support the view that acoustic variation can promote the formation of subspecies.

## Methods

### Sound recording, tegmina measurement, and molecular sampling

In 2013, within 7 days, 40 adults were collected of *Gampsocleis sedakovii* from six localities in Inner Mongolia, northeast China; individuals from CES (Chaersen), BYCG (Bayancuogang), JDM (Jiaodaomu), WCG (Wuchagou), SMJ (Shamajie), and ELC (Elunchun) were also used (Fig 1). The number of calling individuals and the coordinates are shown in Table 1. Calling songs were recorded for each individual, with a digital voice recorder (PCM-D100 Digital Recorder, Sony Corporation, Tokyo, Japan) located at a distance of 20 cm from the singing insect (the distance was consistent). The sampling rate was 96 k-samples/s; S/N ratio was about 40 dB. It was previously reported that the acoustic behaviors and the traits of songs change with temperature (von Helversen 1972), so the environmental temperature for each sound file was recorded to ensure every record was collected within a certain range of ambient temperature.

Morphological structures (e.g., tegmina, pronotum, and body) were measured using 0.01 mm digital vernier calipers. The width of the stridulatory file teeth (WTSTF) was measured under the scanning electron microscope (SEM) (JSM-6510LV, Hitachi Ltd, Tokyo, Japan), and the number of teeth in a stridulatory file (NTSTF) were also counted under SEM. Forty individuals, whose songs had been recorded, were preserved in 70–95% ethanol solution for genetic analyses. Latitude, longitude, and sample number for each locality were also recorded (Table 1).

### Sound analysis

High quality sound samples were selected from all call sequences of each individual for acoustic parameters measurement using the software Cool Edit (Cool Edit pro V2.1, Adobe Systems). To remove the low frequency oscillations, high-pass filtering was performed before analysis. The cutoff frequency was 200 Hz. The song traits of these two subspecies were automatically analyzed using Matlab program (Matlab 7.0,



**Figure 1.** Locations of the six sampling sites in Inn Mongolia, China. Each point signifies a sampling site. Abbreviation: CES, Chaersen; BYCG, Bayancuogang; JDM, Jiaodaomu; WCG, Wuchagou; SMJ, Samajie; ELC, Elunchun.

**Table 1.** The number, geographic coordinates and total number of individuals sampled in acoustic analysis.

No.	Location	N	Longitude (E)	Latitude (N)
1	CES	8	121.9013°	46.4005°
2	BYCG	7	120.3006°	49.2014°
3	JDM	6	121.0001°	50.5005°
4	WCG	7	120.3021°	46.8003°
5	SMJ	6	122.1001°	47.6014°
6	ELC	6	122.4021°	48.2011°

Note: N means the number of samples. The abbreviations of the locations are shown in Figure 1 above.

Mathworks). The spectral analyses were also produced in Matlab using the toll Pwelch and the number of FFT points was 1024. The other parameters were set as default. The selected song traits were pulse duration (PD), pulse interval (PI), pulse repetition rate (PRR), dominant frequency (DF), highest frequency (HF), and lowest frequency (LF).

### **Analysis of genetic differentiation**

Cloning and sequencing of mitochondrial DNA control region within the genus *Gampsocleis* was previously conducted by Zhang, who found that *G. sedakovii* haplotypes clustered into two distinct clades. Total genomic DNA was extracted from the hind femur muscles of 18 insects (selected from the samples obtained the acoustic data). DNA was extracted by a standard phenol-chloroform-isoamyl alcohol (PCI) extraction with slight modification (Sambrook et al. 1989). Amplification of the fragment was performed using the C1-J-1709 (AATTGGWGGWTTYGGAAAYTG) and C1-N-2353 (GCTCGTGTATCTACGTCTATWCC). Each PCR sample contained 5µl of 10 × PCR buffer at pH 8.3 (10 mmol/L of Tris-HCl at pH 8.3, 50 mmol/L KCL), 4 µl of 2.5 mmol/L MgCl<sub>2</sub>, 1.5 U of Taq DNA polymerase, 1 µl of 10 mmol/L of each deoxynucleotide triphosphate (dNTP) (C, G, A, T) all from Takara Biotech (Dalian, China), 2 µl of 10 µmol/L of each primer (Sangon Biotech, Shanghai, China), and 2 µl of DNA template and 33.7 µl ddH<sub>2</sub>O. The regions to be analyzed were amplified using standard PCR approaches with the following conditions: an initial denaturation at 94 °C for 3 min; 32 cycles at 94 °C for 30 sec, primer-specific annealing temperatures 55 °C for 30 sec, extension at 72 °C for 1 min; and final extension for 5 min at 72 °C. This resulted in the amplification of a fragment approximately 644 bp long. The amplicons were sequenced using a BigDye Terminator kit (Applied Biosystems) and an ABI 3730 automated sequencer (Applied Biosystems). Both sense and anti-sense strands were sequenced for all individuals.

### **Cluster analysis**

DNA sequences were aligned using the multiple-sequence program Clustal x 1.8 with parameters setting to default (Thompson et al. 1997). Phylogenetic analyses were performed by using MEGA version 6.0. Phylogenetic trees were reconstructed by neighbour-joining (NJ).

Acoustic and stridulatory files characteristics of *G. sedakovii*, obtained from specimens collected from different locations, were tested by cluster analysis using R Programming Language, respectively. Six traits were used in acoustic cluster analysis, including both aspects of time domain and frequency domain features: PD, PI, PRR, DF, HF, and LF. WL, NTSF, WTSF, LP, BL and WL/LP were contained in this analysis for morphological cluster.

## Results

### Calling Songs between individuals of different sampling sites

Acoustic parameters measured are shown in Table 2. The calling song of the individuals of *G. sedakovii* was continuous, consisting of series of single pulses (Fig 2, 3). In addition, the power spectral density (PSD) was analyzed (Fig 4). Analysis of variance showed that there were significant differences in all song features among the samples captured at different locations (Table 3), and the dissimilarity of samples between locations showed significantly different (Table 4).

### Morphological traits

SEMs as used to determine if the stridulatory files of *G. sedakovii* from specimens of different localities were similar to each other. They were claviform and the teeth in the middle section were wider than those located at both ends of the file (Fig. 5).

In this part of observation, all six morphological traits, except for the number of teeth of a stridulatory file, had significant differences among the other five morphological parameters across the individuals captured from six locations (Table 3 and 5).

### Sequence of mtDNA-COI

Based on the sequence of partial mtDNA (COI), individuals from six locations distinctly formed two separate clades in the NJ analysis. One clade consisted of the individuals from CES, BYCG, and JDM, while the individuals of the other three sites were grouped together (Fig 6). Results suggested that there were some differentiations among these samples collected from different sites at the molecular level. The GenBank accession number is shown in Table 2.

### Cluster results

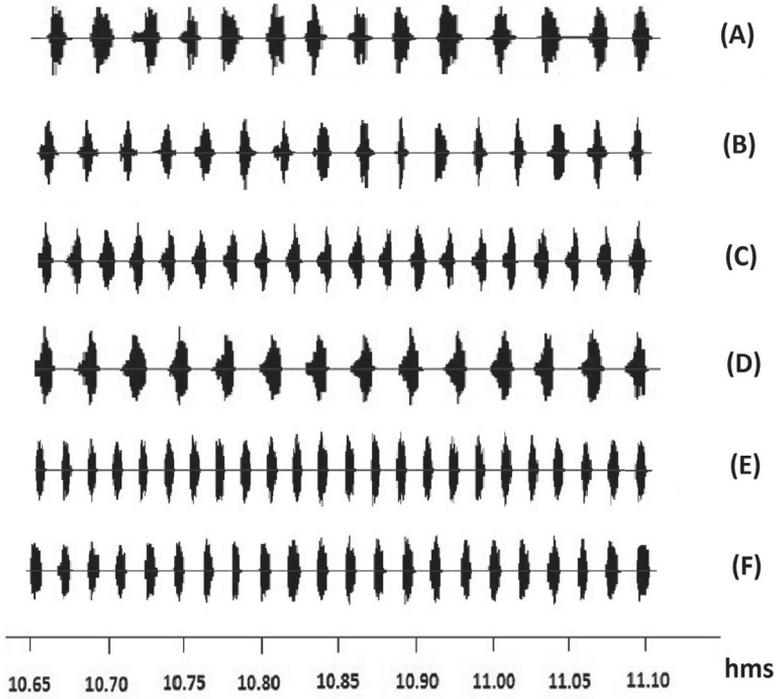
Based on five song traits and six morphological parameters, individuals from the six regions were clustered, based on acoustic traits and morphological parameters respectively, and it was found that the cluster results were consistent with each other. Both cluster results of acoustic signals and morphological features showed there were two main clades among these samples. Specifically, individuals from CES, BYCG, and JDM grouped together and composed one branch. The other branch consisted of the individuals from SMJ, WCG, and ELC (Figs 7 and 8). This result was in accordance with the molecular data. The clustering analyses using the three criteria of acoustics, morphology, and genetic analysis, all gave similar results. Interestingly, through these

**Table 2.** Time-domain and frequency-domain features of *Gampsocleis sedakovii* from six geographic populations.

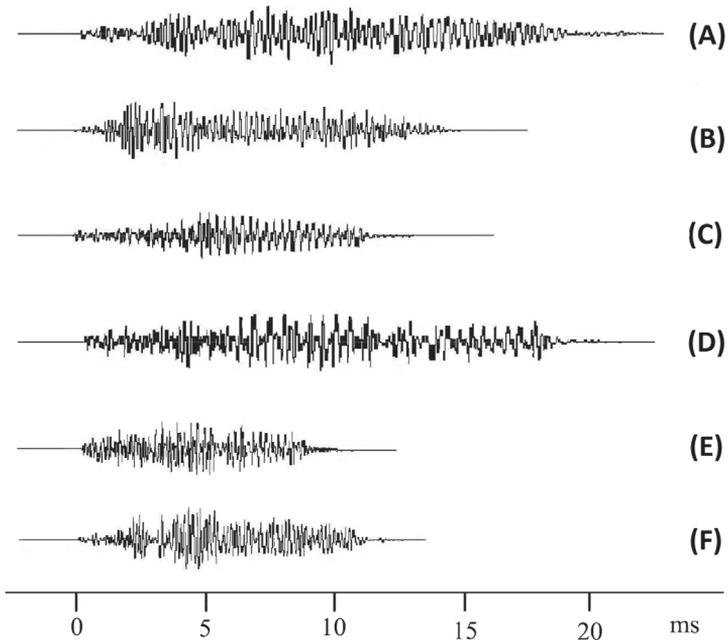
Location	PD (ms)	PI (ms)	PRR	DF (kHz)	HF (kHz)	LF (kHz)	GAN
CES	20.4 ± 0.00	13.1 ± 0.00	0.028 ± 0.00	8.1 ± 0.10	23.7 ± 0.28	5.9 ± 0.09	KT283620 ~ KT283622
BYCG	13.3 ± 0.00	14.1 ± 0.00	0.036 ± 0.00	12.0 ± 0.19	21.0 ± 0.10	7.1 ± 0.09	KT283617 ~ KT283619
JDM	11.8 ± 0.00	10.8 ± 0.00	0.044 ± 0.00	10.8 ± 0.04	22.1 ± 0.07	4.9 ± 0.04	KT283614 ~ KT283616
W/CG	20.1 ± 0.00	12.1 ± 0.00	0.031 ± 0.00	10.6 ± 0.03	19.3 ± 0.15	5.1 ± 0.06	KT283605 ~ KT283607
SMJ	9.4 ± 0.00	9.2 ± 0.00	0.054 ± 0.00	11.1 ± 0.06	19.6 ± 0.07	4.8 ± 0.05	KT283611 ~ KT283613
ELC	10.4 ± 0.00	10.0 ± 0.00	0.049 ± 0.00	8.3 ± 0.26	19.8 ± 0.23	5.1 ± 0.06	KT283608 ~ KT283610

Abbreviation: PD: Pulse duration; PI: Pulse interval; PRR: Pulse repetition rate; DF: Dominant frequency; HF: Highest frequency; LF: Lowest frequency; GAN: GenBank accession number.

Note: the acoustic data were obtained from five individuals from each site; the genetic data are from three individuals included in the acoustic study.



**Figure 2.** The oscillograms of calling songs of *G. sedakovii* collected from six locations at different speeds (A-F: CES, BYCG, JDM, WCG, SMJ and ELC).



**Figure 3.** Presentation of one syllable of calling songs showed in Fig. 2 (A-F: CES, BYCG, JDM, WCG, SMJ and ELC).

**Table 3.** Analysis of variance tables for the analysis of calling song and morphological traits for male *Gampsocleis sedakovii* among six geographic populations.

	Mean Square	d.f.	F	Sig.
PD	0.001	5	188.344	<0.001*
PI	0.000	5	61.899	<0.001*
DF	50.170	5	88.193	<0.001*
HF	113.971	5	1123.716	<0.001*
LF	22.599	5	127.105	<0.001*
WL	351.056	5	1129.041	<0.001*
WTSE	1041.250	5	6.818	<0.001*
NTSE	9.289	5	1.268	0.381
LP	98.797	5	2964.154	<0.001*
BL	1532.304	5	12162.586	<0.001*

\* indicates a significant difference at the 0.05 level.

Abbreviations: PD, pulse duration; PI, pulse interval; DF, dominant frequency; HF, highest frequency; LF, lowest frequency; WL, length of wing; WTSE, width of tooth of a stridulatory file; NTSE, number of teeth of a stridulatory file; LP, length of pronotum; BL, the body length.

**Table 4.** The proximity matrix of analysis of distance of these geographical populations.

	Euclidean Distance					
	CES	BYCG	JDM	WCG	SMJ	ELC
CES	.000	5.925	3.520	14.312	14.889	13.455
BYCG	5.925	.000	3.772	11.254	11.715	11.261
JDM	3.520	3.772	.000	13.255	13.751	12.876
WCG	14.312	11.254	13.255	.000	.950	2.436
SMJ	14.889	11.715	13.751	.950	.000	3.088
ELC	13.455	11.261	12.876	2.436	3.088	.000

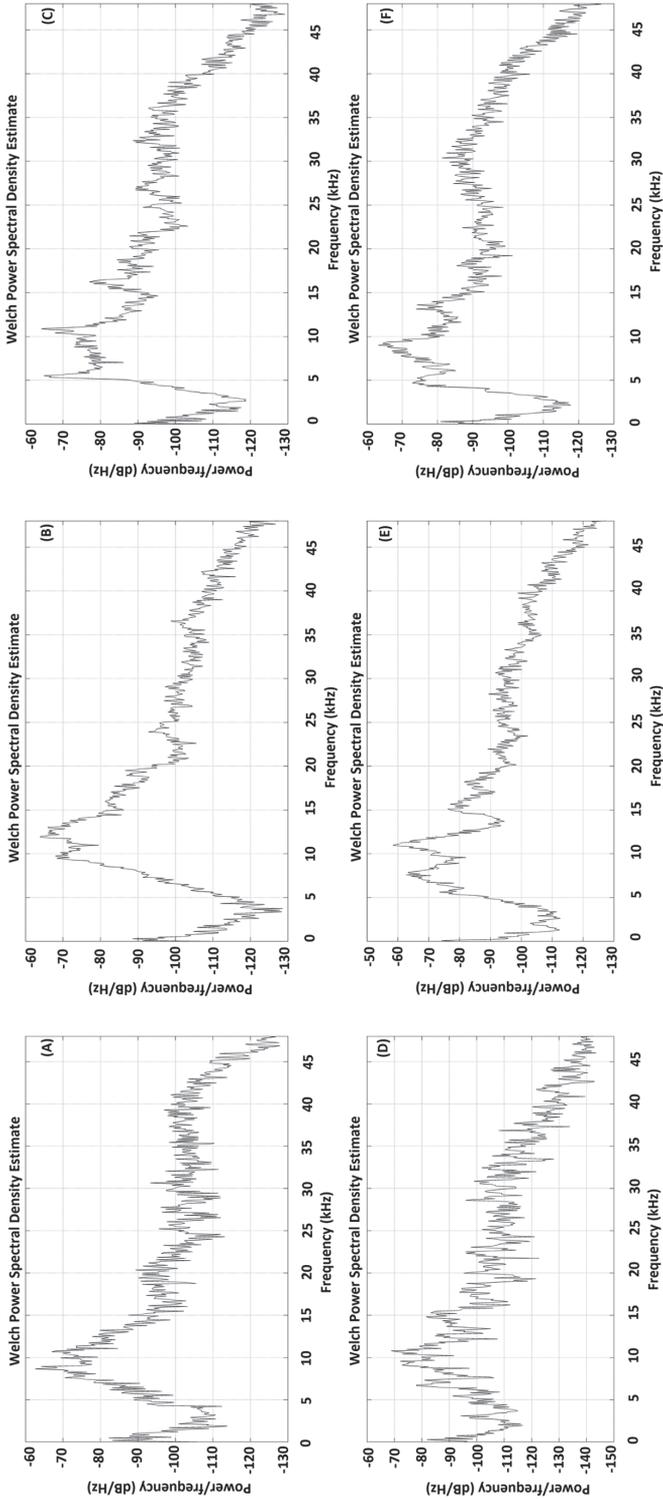
Note: this dissimilarity matrix was obtained by all data including the acoustic, morphological, and genetic information.

**Table 5.** Morphological characteristics of specimens from the different sampling sites.

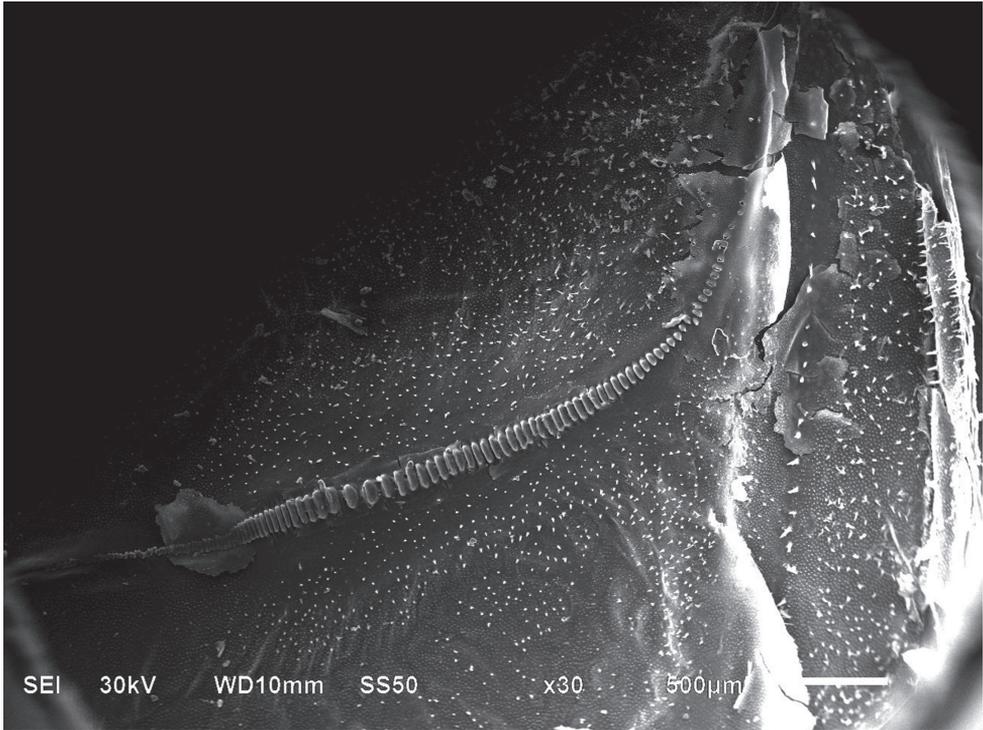
Location	CES	BYCG	JDM	WCG	SMJ	ELC
NTSE	116.7 ± 0.41	115.1 ± 0.49	115.5 ± 0.55	115.6 ± 0.47	115.3 ± 0.54	115.5 ± 0.49
WL (mm)	34.0 ± 0.12	34.0 ± 0.12	34.0 ± 0.12	27.1 ± 0.06	27.3 ± 0.06	28.3 ± 0.05
WTSE (µm)	93.0 ± 3.07	96.0 ± 1.16	93.5 ± 3.08	104.5 ± 0.62	105.2 ± 0.68	103.9 ± 0.44
LP (mm)	7.8 ± 0.02	6.8 ± 0.01	8.7 ± 0.02	8.3 ± 0.01	8.6 ± 0.02	8.5 ± 0.01
BL (mm)	29.1 ± 0.03	24.1 ± 0.04	31.5 ± 0.03	28.5 ± 0.01	33.0 ± 0.03	31.6 ± 0.03
WL/LP	4.1 - 4.4	4.8 - 5.2	3.7 - 4.1	3.1 - 3.2	3.1 - 3.3	3.3 - 3.6

Abbreviations: NTSE, The number of teeth of a stridulatory file; WL, wing length; WTSE, width of tooth of a stridulatory file; LP, length of pronotum; BL, body length.

Note: The wing length was measured from end of the pronotum to the wing tip. The body length was measured from forehead to the end of abdomen.



**Figure 4.** Power spectral density of the calling songs of *G. sedakovii* from six geographic populations (A–F: CES, BYCG, JDM, WCG, SMJ and ELO).



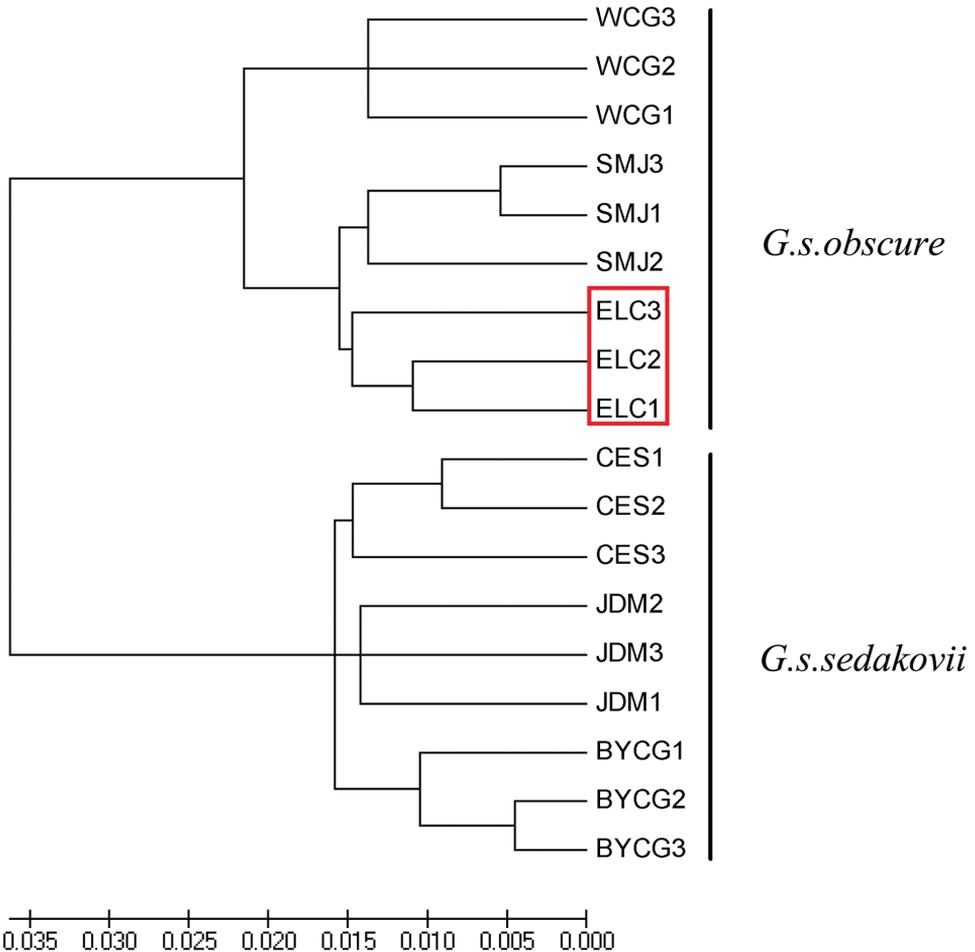
**Figure 5.** SEM of the stridulatory file of *G. sedakovii*.

results, it was found that the *G. sedakovii* from ELC had the median values of all three characteristics. Shown in Table 4, the dissimilarity matrix, the Euclidean distances of ELC were also in the middle.

## Discussion

In this study molecular, acoustic, and morphological differentiation has been analyzed in *G. sedakovii* collected from six sampling sites. By genetic analysis, the individuals from different geographical populations grouped into two clades. This was consistent with the results from the analysis of calling songs and morphological characteristics. For *G. sedakovii*, the morphological features were used to support traditional taxonomy. However, using only morphological traits led to different conclusions and using genetic data, Zhou et al. (2011) showed that the subspecies distinctions did not match precisely the differences in morphology. However, this research supports the view that there are two subspecies of *G. sedakovii* based on morphological features, in accordance with the traditional classification.

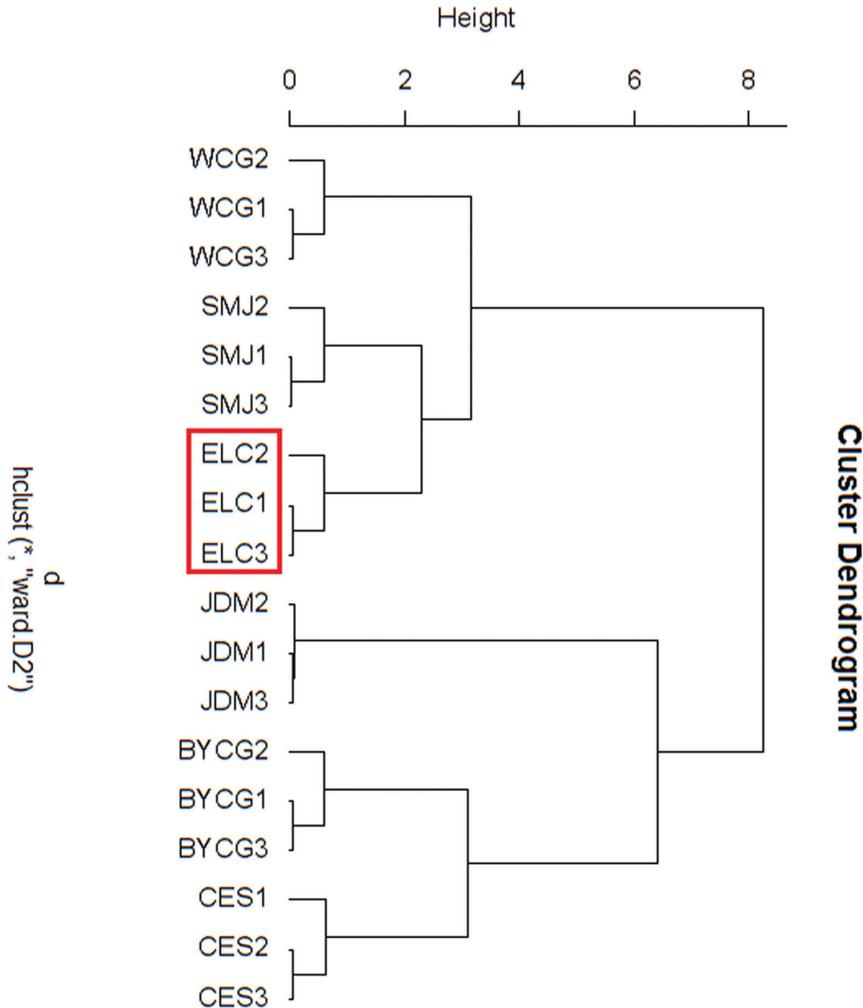
In contrast with these results, the description of the songs of *G. s. sedakovii*, previously made by Wu and Shi (2009), showed that there were two kinds of chirps. We



**Figure 6.** Neighbour-Joining (NJ) tree based on COI sequence from 18 individuals of *G. sedakovii* collected from six sampling sites (CES, BYCG, JDM, WCG, SMJ, and ELC).

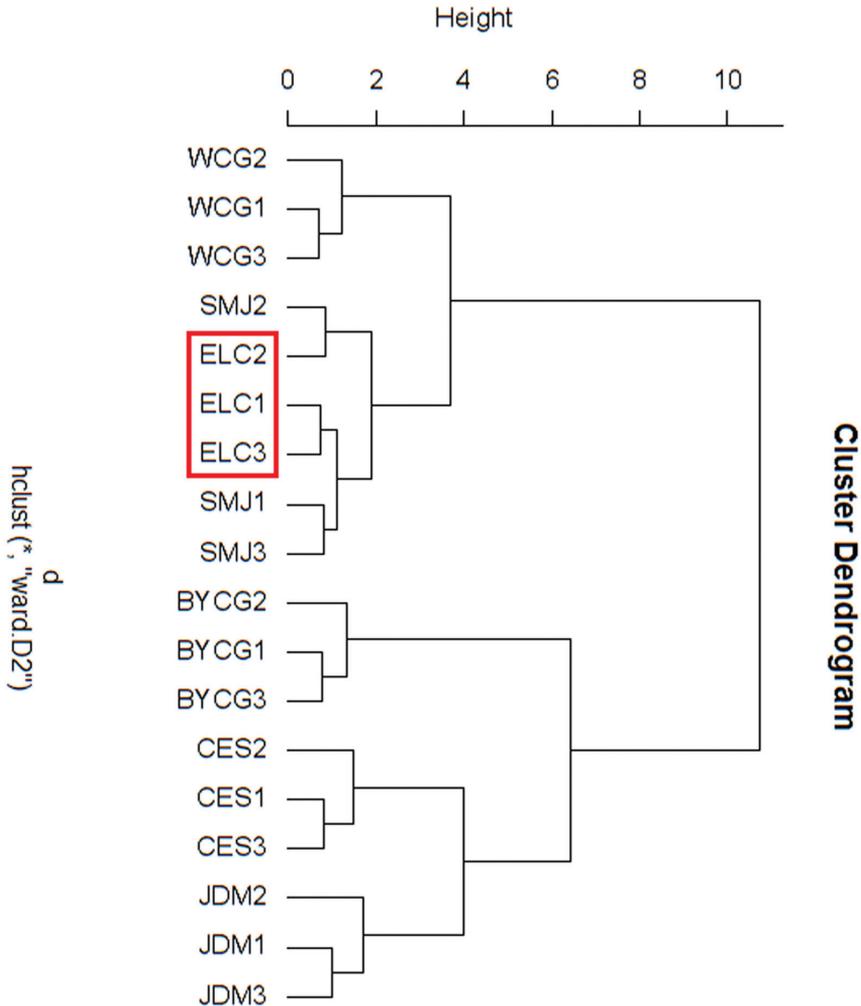
speculate this difference might be related to different sampling sites. The studied species used by Wu and Shi were collected from Hebei province, while we captured the *G. s. sedakovii* in Inner Mongolia area. Different calling songs for different locations might be the result of adaptation to specific habitats.

Evolutionary studies of selected orthopteran taxa have improved our knowledge of the role that insect songs play in speciation (Shaw et al. 2007, Vedenina et al. 2007). The song differentiation of subspecies of *G. sedakovii* remains unknown. Is there a difference between the two subspecies? How much difference was and the cause of this difference remained unknown until now. To increase our knowledge of the evolutionary mechanisms that generate song diversity and the process of subspeciation, it is crucial to study the songs of subspecies. We inferred that the katydid from ELC were the “intermediate type” of *G. sedakovii*. No matter which criteria were applied for



**Figure 7.** Dendrogram generated by cluster analysis based on acoustic characteristics.

classification, these individuals remained intermediate. From the dissimilarity matrix, this phenomenon was also obvious. There were two groups (one for CES, JDM, and BYCG, called group one; the other for WCG, SMJ, and ELC, called group two) and as a whole the Euclidean distance between groups was bigger than within each group. What is noteworthy was that the distances between ELC and group one were smaller compared to the other two sites of group two. Therefore, we inferred it might be the transition to subspeciation. At the same time, we found that the calling songs changed gradually in the process of subspecies formation. In a previous study, the northeast region of China was thought to be the centre of differentiation of *G. sedakovii* (see Bey-Bienko 1930). In the process of diffusion, evolution took the form of radiation, so we conclude that ELC was closer to the centre of differentiation.



**Figure 8.** Dendrogram generated by cluster analysis based on morphological traits.

In the study of *Apis cerana*, the discovery of the new species showed that the classification of subspecies need not be based on differences in geographical region (Zhuang 1989). However, although distributed in geographically close regions, individuals might belong to different subspecies.

In other animal groups, such as frogs (Amézquita et al. 2009, Funk et al. 2009, Velásquez et al. 2013), birds (Irwin et al. 2008), and some primates (Thin et al. 2011, Meyer et al. 2012), positive correlations between bioacoustic traits and genetic differences have been reported. Jaiswara et al. (2012) showed that the phylogenetic analyses largely supported the acoustic clusters for the genus *Itaropsis*, and these two lineages were further supported with morphological variation. Our data supports

the idea that the structure of acoustic signals is closely related to genetic differences among populations and provides some evidence that this relationship exists on the subspecies level.

In summary, this study shows that there are two lineages within the species *G. sedakovii*. This conclusion supports the existing classification with two subspecies. Further examination, including samples from more geographical populations, will be needed for a more robust assessment of phylogenetic analysis.

## Conclusions

Two large groups within species *G. sedakovii* were discovered by performing genetic, morphological, and acoustic analysis. Our data justifies the existing classification of *G. sedakovii* into two subspecies, *G. s. sedakovii* and *G. s. obscura*. We found the calling songs differed with geographical distribution, suggesting that acoustic variation might play an important role in the formation of new subspecies.

## Acknowledgments

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# Congruence between cytochrome oxidase I (COI) and morphological data in *Anuraphis* spp. (Hemiptera, Aphididae) with a comparison between the utility of the 5' barcode and 3' COI regions

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## Abstract

The discrimination of species in the genus *Anuraphis* is particularly difficult due to the overlap of morphological characters. In this study, we used the 5' (barcode) and 3' regions of cytochrome oxidase I (COI) to test their utility in the identification of species in this genus as well as closely related species. Both regions were useful to discriminate all the species tested. However the non-barcode 3' region resulted in higher resolution and support for species relationships when the data were analyzed using both Maximum Likelihood and MrBayes. We propose the development of an integrated database that encompasses morphological, molecular, life-cycle, host plant and bibliographic information to facilitate and increase the accuracy of aphid identification.

## Keywords

Insects, aphids, taxonomy, species identification

## Introduction

Aphids are sap-sucking insects. Currently there are 5012 valid species (Favret 2014) associated with plants belonging to various botanical groups. Many species have a heteroecious life cycle that includes alternating between a primary host plant (usually a tree) and a secondary host (usually an herbaceous species). The genus *Anuraphis* Del Guercio presently ascribed to the tribe Macrosiphini includes a small number of taxonomically well-defined species, *A. subterranea* (Walker, 1852), *A. farfarae* (Koch, 1854), *A. catonii* Hille Ris Lambers, 1935, *A. pyrilaseri* Shaposhnikov, 1950, *A. cachryos* Barbagallo & Stroyan, 1982, *A. ferulae* Shaposhnikov, 1995 and *A. shaposhnikovii* Barbagallo & Cocuzza, 2003. In addition, Remaudière and Remaudière (1997) reported four other nominal species (i.e., *A. capparidis* Nevsky, 1929, *A. cortusae* Nevsky, 1929, *A. floris* Monzen, 1934 and *A. katsurae* Shinji, 1952). However, the generic placement of *A. capparidis* has been questioned by Blackman and Eastop (2006) who noted that, based on the original description, this is probably not an *Anuraphis* species but an immature *Aphis* sp. The recognized *Anuraphis* species are distributed in the Ponto-Mediterranean area of the western Palearctic region. A common trait of almost all *Anuraphis* species is the use of Apiaceae as host plants, with the exception of *A. farfarae* that feeds on Asteraceae (*Tussilago*, *Petasites* and *Hieracium*). Some populations of *A. subterranea*, *A. pyrilaseri*, *A. farfarae* and *A. catonii* have been shown to be heteroecious holocyclic with *Pyrus* spp. (Rosaceae) as primary host plants (Shaposhnikov 1951; Kolesova 1972; Lampel and Meyer 2007). However, some populations of *A. farfarae* (Shaposhnikov & Sharov, 1978), and probably other species, are solely anholocyclic on secondary host plants. For *A. cachryos*, *A. shaposhnikovii* and *A. ferulae* the primary host plants remain to be determined.

*A. farfarae* (pear-colt's foot aphid) and *A. subterranea* (pear-hogweed aphid) have been reported in the literature as pests of pear, where they cause direct damage to young foliage in spring (Kolesova 1972). However, damage due to their infestation has a negligible effect on production (Alford 2014).

All species belonging to the genus *Anuraphis* are morphologically similar to each other but easily discriminated from other genera. The main morphological features of the genus are an almost flat frontal profile, as a result of the minimally developed antennal tubercles, and a short cauda. Moreover, *Anuraphis* shares with a few other genera of Macrosiphini a typical spinulose ornamentation of siphunculi and a well-developed, often almost complete set of dorsal tubercles (both marginal and spinal). However, as already reported for other groups of aphids, the morphometric similarity among *Anuraphis* species leads to an overlap that renders their discrimination to species level difficult (Stroyan 1984; Heie 1986). Barbagallo and Cocuzza (2003) published a morphological key to discriminate viviparous morphs (for both apterae and alate) of *Anuraphis* species and a discriminant function to separate *A. subterranea* and *A. shaposhnikovii*. However, the discrimination of *A. subterranea* and *A. shaposhnikovii* using only morphological characters requires the skills of an experienced researcher, especially when specimens are collected on primary host plants or when the secondary host is unknown.

In some genus (e.g. *Aphis*), a recurrent and difficult problem in using only morphological characters to identify aphids is that for many species there are insufficient diagnostic characters, resulting in their identification being partially based on host plant association and life cycle characteristics (Stroyan 1984; Heie 1986). However, due to incomplete and/or missing knowledge of many aphid/plant associations, the use of this criterion to identify aphid species, could lead to misidentification (Stroyan 1984; Coeur d'acier et al. 2007). Many studies have used the 5' region of the cytochrome oxidase I gene (COI), more commonly referred to as the DNA barcode region, as a useful tool to discriminate various groups of insects (Hebert et al. 2003a, b, Deng et al. 2012; Derocles et al. 2012; Williams et al. 2012; Julsirikul et al. 2013), including aphid species (Coeur d'acier et al. 2008; Foottit et al. 2008, 2009a, b, c; Miller and Foottit 2009; Wang and Qiao 2009; Kim et al. 2010; Lee et al. 2011; Zhang et al. 2010, 2011; Wang et al. 2011; Chen et al. 2013; Massimino Cocuzza and Cavalieri 2014). However, especially in some insect groups such as Aphididae, the DNA barcode region, due to low genetic diversity at this marker, was no more informative than morphological characters (Foottit et al. 2008; Lee et al. 2011). For instance, results obtained using the COI barcode region with adelgids were inadequate for the purpose of discriminating species that were morphologically indistinguishable or belonged to a species-complex (Žuroková 2010). Other studies have shown that the COI barcode region discriminated 96% of aphid taxa tested (Foottit et al. 2008).

Ideally the description of a species should result from a synthesis of information that encompasses morphological, molecular, biological, biogeographical, physiological, ecological and bibliographical data (Dayrat 2005; De Salle 2006; Waugh 2007; Padial et al. 2010; Taylor and Harris 2012), however, this compendium of information is lacking for the great majority of species.

This study was undertaken to improve the current taxonomic knowledge of the various taxa belonging to the genus *Anuraphis* by testing the utility of the COI gene, specifically comparing the widely used barcode 5' region with the much less studied 3' region, as a molecular tool for their identification. A further goal is to compare the results obtained with the COI gene to those previously published using only morphological characters (Barbagallo and Cocuzza 2003).

## Materials and methods

This study was conducted with seven species (Table 1) belonging to the genus *Anuraphis*. Unfortunately, it was not possible to include *A. ferulae*, a species recorded only from Tajikistan on *Ferula* sp. When possible, species were collected in different geographic locations and on different host plants. Taxonomic nomenclature follows Remaudière and Remaudière (1997). Two samples of *Nearctaphis bakeri* (Cowen, 1895) were included in the analysis. The genus *Nearctaphis* is considered the vicariant (or sister) Nearctic relative of *Anuraphis*, from which it differs morphologically due to the lack of spinal tubercles, and biologically by the use of *Malus* sp. as a primary host plant

Table 1. Summary of information on samples used in the molecular analysis.

Voucher code	Species	Host plant	Location	Sampling date	GeneBank accession N°
S03189	<i>Anuraphis farfarae</i> Koch	<i>Tussilago farfara</i>	40,0970N/15,8131E Lauria (Porezza, Basilicata)	25 Jun. 03	KT878791
S03190	<i>A. farfarae</i>	<i>Tussilago farfara</i>	39,8762N/16,0050E Mormanno (Cosenza, Calabria)	25 Jun. 03	KT878792
S13572	<i>A. farfarae</i>	<i>Tussilago farfara</i>	46,5606N/12,1285E Cortina d'Ampezzo (Bolzano, Trentino Alto Adige)	18 Sep. 13	KT878793
S03157	<i>A. pyrilaserei</i> Shaposhnikov	<i>Maquydaris pastinacea</i>	37,9795N/12,7637E Buseo Palizzolo (Trapani, Sicily)	6 Jun. 03	KT878794
S03171	<i>A. pyrilaserei</i>	<i>Thapsia garganica</i>	37,9258N/15,7602E Rognudi (Reggio Calabria, Calabria)	9 Jun. 03	KT878795
S03141	<i>A. pyrilaserei</i>	<i>Ferula communis</i>	37,6345N/15,0744E Trecastagni (Catania, Sicily)	15 May 03	KT878797
S03146	<i>A. pyrilaserei</i>	<i>Ferula communis</i>	38,0229N/15,3890E Fiumedinisi (Messina, Sicily)	17 May 03	KT878799
S03152	<i>A. pyrilaserei</i>	<i>Thapsia garganica</i>	37,8152N/15,1869E Piedimonte Etneo (Catania, Sicily)	28 May 03	KT878796
S03147	<i>A. pyrilaserei</i>	<i>Ferula communis</i>	38,0440N/15,4309E Itala (Messina, Sicily)	17 May 03	KP714117
CBGP#ACOE2024	<i>A. pyrilaserei</i>	Not reported	37,7863N/15,2337E Fiunefreddo (Catania, Sicily)	27 May 06	ACEA860
GBMIN37806	<i>A. pyrilaserei</i>	Not reported	Not reported	Not reported	GU568501
CBGP#ACOE2050	<i>A. pyrilaserei</i>	Not reported	37,7826N/15,1325E Sant'Alfo (Catania, Sicily)	30 May 06	ACEA880
CBGP#ACOE1998	<i>A. pyrilaserei</i>	Not reported	37,7827N/15,1418E Linguaglossa (Catania, Sicily)	23 May 06	ACEA839
S03144	<i>A. catonii</i> HRL	<i>Pimpinella major</i>	38,0505N/15,4343E Itala (Messina, Sicily)	17 May 03	KT878815
S03173	<i>A. catonii</i>	<i>Pimpinella peregrina</i>	37,9937N/15,9250E Boya (Reggio Calabria, Calabria)	9 Jun. 03	KT878816

Voucher code	Species	Host plant	Location	Sampling date	GeneBank accession N°
S12477	<i>A. catonii</i>	<i>Pimpinella peregrina</i>	37,1334N/15,0165E Sortino (Siracusa, Sicily)	25 May 12	KT878817
S03179	<i>A. cachryos</i> Barb. & Str.	<i>Cachrys sicula</i>	37,3619N/15,0219E Scordia (Catania, Sicily)	15 Jun. 12	KT878818
S03180	<i>A. cachryos</i>	<i>Cachrys sicula</i>	36,7765N/14,5989E Donnalucata (Ragusa, Sicily)	15 Jun. 12	KT878819
S12423	<i>A. cachryos</i>	<i>Cachrys sicula</i>	36,7766N/14,5990E Donnalucata (Ragusa, Sicily)	2 May 12	KT878820
S14599	<i>A. cachryos</i>	<i>Cachrys libanotis</i>	37,3080N/14,8587E Lentini (Siracusa, Sicily)	13 Jun. 13	KT878821
CPGP#ACOE1057	<i>A. cachryos</i>	Not reported	42,7869N/3,0361 Languedoc-Roussillon (France)	30 Oct. 00	ACEA353
S03181	<i>A. subterranea</i> (Walker)	<i>Heracleum pyrenaicum</i>	37,9756N/14,9516E Floresta (Messina, Sicily)	22 Jun. 03	KT878800
S03182	<i>A. subterranea</i>	<i>Heracleum pyrenaicum</i>	37,9808N/15,1435E Novara di Sicilia (Messina, Sicily)	22 Jun. 03	KT878801
S12517	<i>A. subterranea</i>	<i>Heracleum sphondylium</i>	37,9020N/13,9999E Isnello (Palermo, Sicily)	3 Jul. 12	KT878804
S03191	<i>A. subterranea</i>	<i>Pastinaca sativa</i>	39,8761N/16,0038E Mormanno (Cosenza, Sicily)	25 Jun. 03	KT878805
S03163	<i>A. subterranea</i>	<i>Heracleum pyrenaicum</i>	37,8801N/14,0283E Perralia Sortana (Palermo, Sicily)	6 Jun. 03	KT878802
S03184	<i>A. subterranea</i>	<i>Heracleum pyrenaicum</i>	37,9756N/14,9516E Floresta (Messina, Sicily)	22 Jun. 03	KT878803
CBGP#ACOE2053	<i>A. subterranea</i>	Not reported	37,9216N/14,957E Randazzo (Catania, Sicily)	30 May 06	ACEA883
CBGP#ACOE2060	<i>A. subterranea</i>	Not reported	37,9921N/14,9306E Floresta (Messina, Sicily)	30 May 06	ACEA890
CBGP#ACOE645	<i>A. subterranea</i>	Not reported	44,8893N/1,4062E Peryllac-et-Millac (France)	2 Jun. 99	ACEA164
CBGP#ACOE1068	<i>A. subterranea</i>	Not reported	42,8742N/2,1829E Quillan (France)	21 May 01	ACEA367

Voucher code	Species	Host plant	Location	Sampling date	GeneBank accession N°
S03160	<i>A. shaposhnikovi</i> Barb. & Coc.	<i>Maquydaris pastinacea</i>	37,9795N/12,7637E Buseto Palizzolo (Trapani, Sicily)	6 Jun. 03	KT878808
S03143	<i>A. shaposhnikovi</i>	<i>Opopanax chironium</i>	37,9075N/15,1211E Francavilla di Sicilia (Messina, Sicily)	16 May 03	KT878809
S03166	<i>A. shaposhnikovi</i>	<i>Opopanax chironium</i>	37,9917N/15,9309E Bova Sup. (Reggio Cal., Calabria)	9 Jun. 03	KT878810
S14589	<i>A. shaposhnikovi</i>	<i>Opopanax chironium</i>	37,6324N/14,9859E Belpasso (Catania, Sicily)	21 Apr. 14	KT878811
CBGP#ACOE438	<i>A. shaposhnikovi</i>	Not reported	44,1891N/6,7477E Entraunes (France)	24 Jul. 98	ACEA035
CBGP#ACOE2052	<i>A. shaposhnikovi</i>	Not reported	37,9216N/14,957E Randazzo (Catania, Sicily)	30 May 06	ACEA882
S12413	<i>Nearctaphis bakeri</i> (Cowen)	<i>Trifolium pratense</i>	45,0877N/7,6387E Torino (Piemonte)	16 Apr. 12	KT878807
S13562	<i>N. bakeri</i>	<i>Trifolium pratense</i>	41,2367N/13,9319E Sessa Aurunca (Caserta, Campania)	12 Jun. 13	KT878806
CBGP#ACOE824	<i>N. bakeri</i>	Not reported	43,7337N/3,5500 Saint-Guillerm-le-Desert (France)	8 Apr. 00	ACEA242
CBGP#ACOE1020	<i>N. bakeri</i>	Not reported	47,9862N/-4,4642E Plouhinec (France)	30 Jul.00	ACEA331
S06340	<i>Aphis fabae</i> Scopoli	<i>Vicia faba</i>	36,9251N/14,7423E Ragusa (Sicily)	20 Apr. 06	KT878822
CBGP#ACOE460	<i>A. fabae</i>	Not reported	44,0105N/3,6058E Levignan (France)	1 Jul. 98	ACEA050
S04230	<i>Roepkea marchali</i> HIRL	<i>Prunus mahaleb</i>	43,2235N/13,1518E S. Severino (Macerata, Marche)	20 May 04	KT878812
S14613	<i>R. marchali</i>	<i>Prunus mahaleb</i>	50,0810N/14,4029E Prague (Czech Rep.)	31 May 14	KT878813

Voucher code	Species	Host plant	Location	Sampling date	GeneBank accession N°
S14623	<i>R. marchali</i>	<i>Prunus mahaleb</i>	50,0871N/14,4172E Prague (Czech Rep.)	1 Jun. 14	KT878814
CBGP#ACOE1674	<i>R. marchali</i>	Not reported	43,6833N/3,9262E Teyran (France)	26 Jun. 0	ACEA723
S03145	<i>Brachycaudus jacobii</i> Stroyan	<i>Myosotis sylvatica</i>	38,0505N/15,4343E Itala (Messina, Sicily)	15 May 03	EU189690
GBMIN10086	<i>B. jacobii</i>	<i>Myosotis sylvatica</i>	38,0505N/15,4343E Itala (Messina, Sicily)	15 May 03	EU196598

and Fabaceae and Scrophulariaceae as secondary hosts (Hille Ris Lambers 1970). In addition, samples of *Roepkea marchali* Hille Ris Lambers, *Brachycaudus jacobii* Stroyan and *Aphis fabae* Scopoli, were used as out-groups. Collections of aphid colonies were made on individual plants and at least two individuals were sequenced per collection. Details regarding the specimens used in this study (host plants, collection locality, sampling date and gene bank accession numbers) can be found in Table 1. For each sample, 5–6 apterae and alate individuals were slide-mounted for morphological identification. Specimens were morphologically identified by S. Barbagallo using characters in the keys provided by Heie (1992), Barbagallo and Cocuzza (2003) and Blackman (2010). Specimen slides are stored in the Aphididae collection of S. Barbagallo (Department of Agriculture, Food and Environment, University of Catania).

Whole aphid specimens for DNA sequencing were stored in 95% ethanol at -20 °C, those used for morphological observations were stored in 70% ethanol and at room temperature.

Total genomic DNA was extracted by macerating entire single individuals using the DNeasy Blood & Tissue kit (Qiagen®, Hilden, Germany) in 50 µl of extraction buffer and stored at -20 °C. To compare the utility of the 5', barcode region, and the 3' region of COI we amplified the following regions: for the 5' end, a 600 bp region using primers LCO1490 and HCO2198 (Folmer et al. 1994), widely used on a variety of organisms as well as aphids (Hebert et al. 2003, Coeur D'acier et al. 2008; Kim et al. 2010; Lee et al. 2014), for the 3' end, a 648 bp fragment using primers C1-J-2195 and TL2-N-3014 (Simon et al. 1994), found to be informative in several aphid studies (Coeur d'acier et al. 2008; Massimino Cocuzza and Cavalieri 2014). PCR reactions were performed using 8.5 µl of buffer premix 2x F (FailSafe™ PCR Premix Selection Kit –Epicentre Technologies) 1 µl of each primer (10 µM), 0.5 µl Taq polymerase (Life Technologies) and 2 µl DNA template (quantified in 6–18 ng/ µl) in a total volume of 21 µl. The cycle conditions for primer set LCO1490 and HCO2198 was 94 °C for 3 min (initial denaturation), followed by 35 cycles of 94 °C for 30 s (denaturation), 48 °C for 1 min (annealing) and 72 °C for 1 min (extension). Primer set C1-J-2195 and TL2-N-3014 conditions were 96 °C for 5 min (initial denaturation) and 35 cycles of 96 °C for 5 s (denaturation), 45 °C for 1 min (annealing), 72 °C for 1 min (extension). PCR products were run in 1.6% agarose gels stained with Syber Safe DNA gel stain (Life Technologies). PCR products were sequenced at BMR genomics (Padua, Italy) or at the W. M. Keck Center at the University of Illinois (Urbana-Champaign, IL) and run on an ABI PRISM 3730XL DNA analyzer (Life Technologies Corporation, Carlsbad, CA, USA). For each sample 2–8 individuals were sequenced, and one representative sequence for each sample was subsequently chosen. Sequences of *Anuraphis* available in Genbank and or BOLD databases were utilized in the analysis and are identified in Table 1 by their accession number.

The COI sequences were edited manually using BioEdit (Hall 1999) or Sequencher v. 5.0 (GeneCodes Corporation, AnnArbor, MI, USA). Nucleotide sequences were translated using EPoS (Griebel et al. 2008) to check for stop codons (Zhang and Hewitt 1996). Sequence divergences were calculated using the *p*-distance model as suggested by

Srivathsan and Meier (2012), and a neighbour-joining (NJ) tree (Saitou and Nei 1987), as implemented in MEGA 6 (Tamura et al. 2011), was used to visualize the distance matrix among taxa and population samples. The Bayesian phylogenetic analysis was conducted using Mr.Bayes v 3.2.1 (Ronquist et al. 2012) implementing the GTR + I model of sequence evolution selected by JModel test 2.1.4 (Posada 2008) based on the Akaike information criterion (AIC). Beginning with random trees, four independent runs with four Markov chains were run for 25,000,000 generations. Bayesian trees were sampled every 1000<sup>th</sup> generations. All other parameters were set at default. Convergence was assessed using TRACER 1.6 (Rambaut et al. 2014) using a 25% burn in value. Posterior probabilities (pp) and the consensus trees were computed in MrBayes. The Bayesian analysis was run on the CIPRES Science Gateway (Miller et al. 2010). A maximum likelihood analysis was also performed using RAxML v. 8 (Stamatakis 2014) with the GTR +I model; clade support for the maximum likelihood tree was determined in RAxML by bootstrap, based on 1000 pseudoreplicates.

## Results

COI was easily amplified for all specimens analysed using the primers indicated above. No frame shift or premature stop codons were detected.

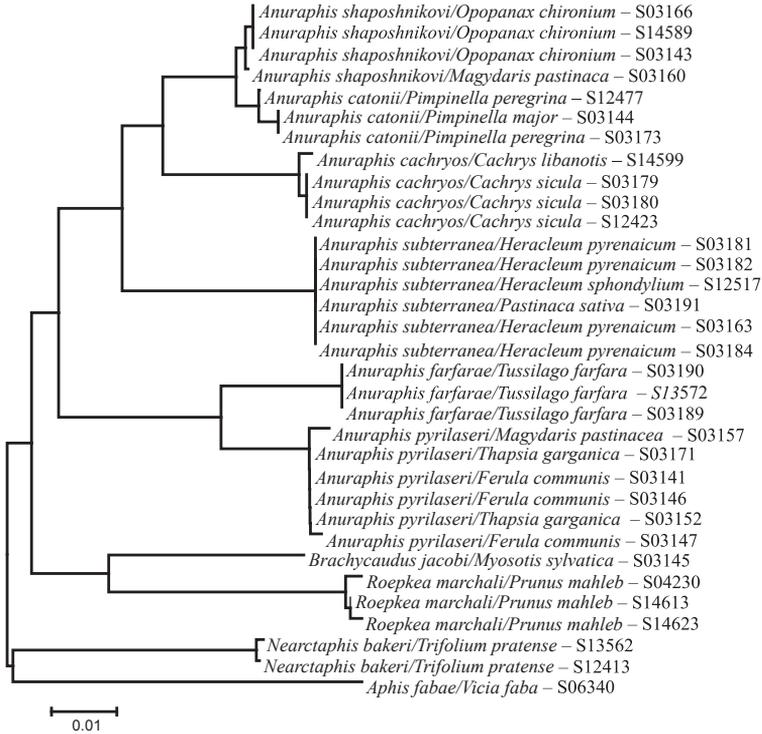
The five prime end (5') constituted a 601 base pair (bp) fragment. With total bp frequencies of 75.3% for A/T and 24.7% for G/C. These latter results concur with those found for other aphid species (Shufran et al. 2000; Wang et al. 2011). The 5' end showed that there were 533 conserved and 125 variable nucleotides with 92 of the latter being parsimony informative. The overall average distance for the 5' end of the COI gene was 5.8, ranging from 0 (samples within a species) to 11.7 across species.

The three prime end (3') sequences analysed consisted of 648 bp with frequencies of 74.9% A/T and 25.1% G/C. The 3' end showed that there were 521 constant and 127 variable sites of which 111 were parsimony informative. The percentage of variable sites was slightly higher for the 3' (19.6%) than the 5' end (18.99%).

Considering the 5' region, the mean genetic distance of *Anuraphis* species from *N. bakeri*, *R. marchali*, *B. jacobi* and *A. fabae* were 6.5%, 6.7%, 8.0% and 9.2%, respectively, whereas slightly higher distance values were observed for most comparisons of the 3' region (7.5%, 7.9, 8.1 and 8.6%, respectively). The genetic differences recorded in the 5' barcode region among *Anuraphis* species (Table 2) ranged from 0.2% (between *A. shaposhnikovii* and *A. catonii*) to 6.7% (between *A. cachryos* and *A. pyrillaseri*). When the 3' region was used, the pairwise distance ranged from 0.8 (*A. shaposhnikovii* vs *A. catonii*) to 7.4 (*A. subterranea* vs *A. pyrillaseri*).

Our results indicate that there is high genetic homogeneity within *Anuraphis* species, despite differences in geographic origin and host plant. *Anuraphis farfarae* is the only member of the genus that uses Asteraceae, nevertheless its position in *Anuraphis* is well supported (Fig. 2c and 2a). Adaptation to this host plant may be of recent origin and its ecological uniqueness is not reflected at the COI level.

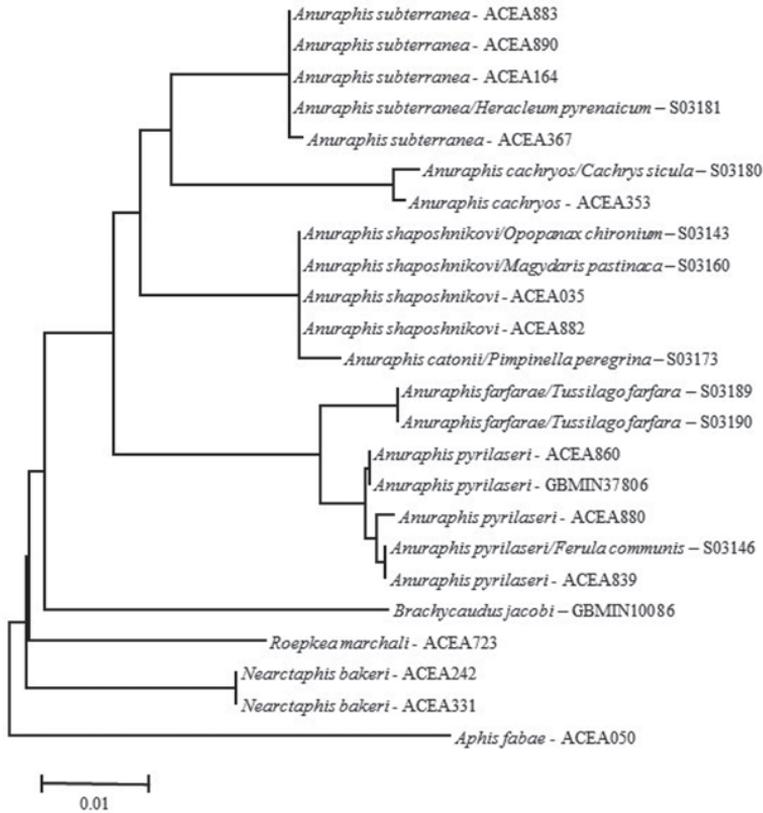




**Figure 1a.** Neighbor-Joining tree showing relationships among selected *Anuraphis* species estimated using 648 bp at the 3' end of the COI mitochondrial gene. Distance were estimated using the *p*-distance model of sequence evolution.

Little to no intraspecific differences were found among the various geographic samples of each *Anuraphis* species (0.3% only for some populations of *A. catonii*, *A. cachryos* and *A. pyrilaseri*). Phylogenetic analysis with Neighbour Joining (NJ), Maximum Likelihood (ML) and Bayesian (MrBayes) using the 5' and 3' end of the COI gene showed two discreet clades: one comprising *A. farfarae* and *A. pyrilaseri*; the other including *A. cachryos*, *A. subterranea*, *A. catonii*, and *A. shaposhnikovii* respectively (Figs 1, 2).

The clade including *A. farfarae* and *A. pyrilaseri* shows a genetic distance between the two species of 3.2% when using the 3' end and 1.7% when using the 5' end of COI. The various samples of *A. farfarae* were highly similar, regardless of host plant, locality and COI region examined. Similarly, the populations of *A. pyrilaseri* showed low genetic variability (0.3%). Differences in body colour, possibly due to host plant effects, as well as differences in dorsal abdominal sclerotisation, do not correlate with the low genetic diversity observed with the COI gene. The various samples of *A. subterranea* showed no genetic differences, regardless of their geographic origin, host plant or COI region used for the analysis. Genetic difference (3.7% with 3' and 4.7% with 5' region) between *A. subterranea* and *A. shaposhnikovii* clearly distinguishes the two species, despite the small morphological differences observed (length of ultimate rostral



**Figure 1b.** Neighbor-Joining tree showing relationships among selected *Anuraphis* species estimated using 658 bp at the 5' end of the COI mitochondrial gene. Distance were estimated using the *p*-distance model of sequence evolution.

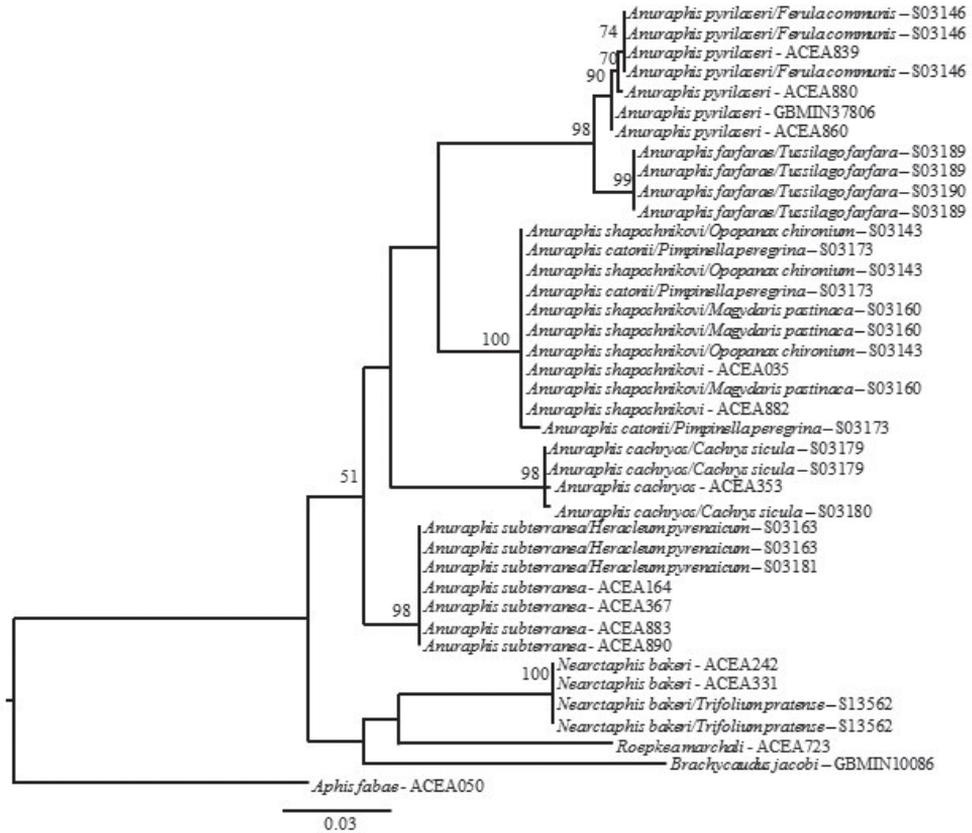
segment and number and distribution of abdominal spinal tubercles). *A. shaposhnikovi* and *A. catonii* showed the lowest genetic divergence (<1%) regardless of the COI region considered. However, while with 5' COI barcode showed a pairwise distance of 0.2%, the 3' region showed a difference of 0.8%.

A result similar to the one based on COI was found using a multivariate discriminant analysis with 16 morphometric characters (Barbagallo and Cocuzza 2003) and graphically as Mahalanobis' generalized distance (Fig. 3). The dendrogram indicates a distinction of *A. subterranea* and *A. shaposhnikovi*, and the similarity between the latter species and *A. catonii*.

## Discussion

The molecular analysis based on the 3' and 5' COI gene regions indicates that the genus *Anuraphis* is a homogeneous taxonomic group. However, COI also provides

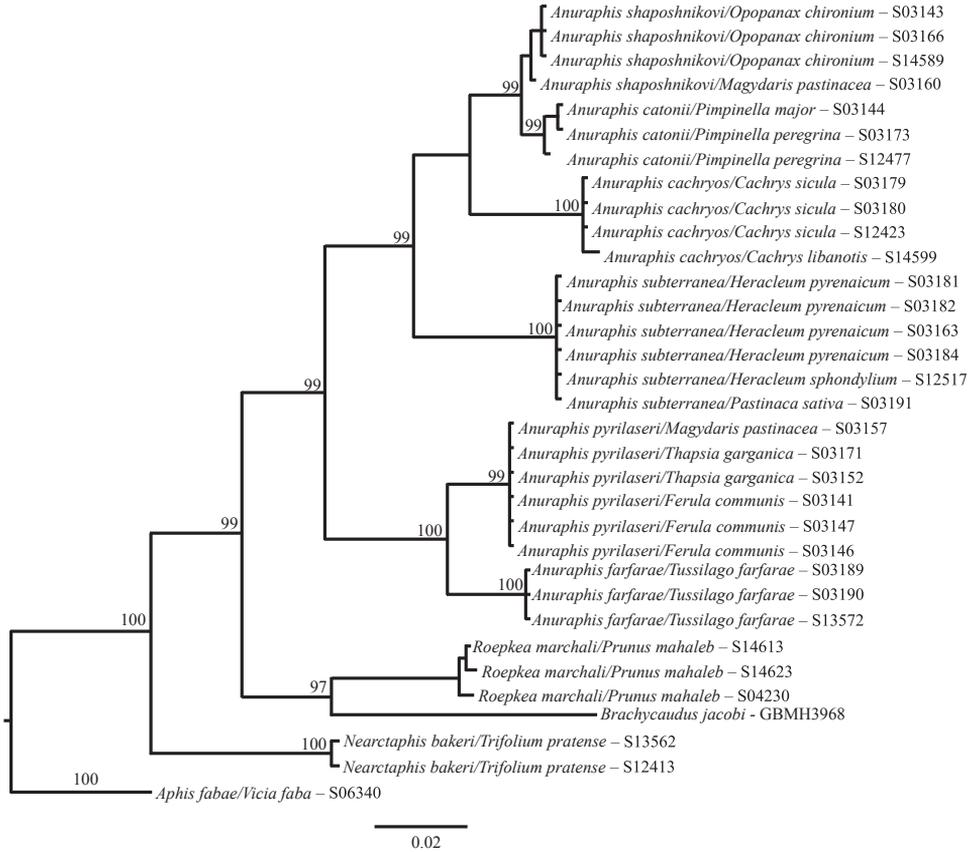




**Figure 2b.** Likelihood tree estimated using 658 bp at the 5' end of COI for selected *Anuraphis* species.

shown that when transferred to *Pastinaca sativa*, the nymphs of *A. catonii* can reach adulthood (Stroyan 1959); conversely, Shaposhnikov (1951) observed that nymphs of *A. catonii* transferred from pear survive on *Pimpinella* sp. but not on *Pastinaca sativa*. A further intricacy was the recovery by Kolesova (1972) of a sample of *A. catonii* on *P. sativa*, although this could be a case of misidentification.

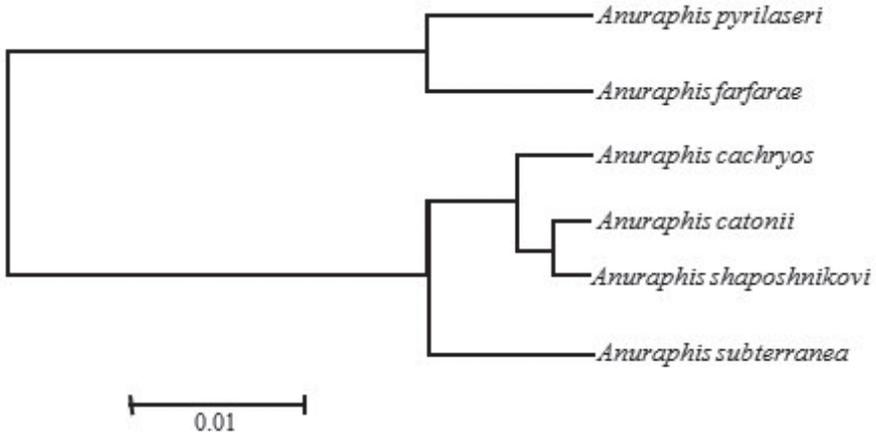
Barbagallo and Cocuzza (2003) reported that *A. shaposhnikovii*, collected on *Magydaris pastinacea* has slight morphological differences from those developing on *Opopanax chironium*, (*i.e.*, the length of the last rostral segment and the number of abdominal spinal tubercles). The putatively fixed nature of the morphological differences is confirmed by the COI analysis and can be the result of intraspecific variability and possibly geographic isolation, since *M. pastinacea* occurs in very restricted areas of Sicily and Sardinia. Another interesting observation is the low genetic divergence observed between *A. catonii* and *A. shaposhnikovii*, a similarity already evidenced in the morphological analysis (Barbagallo and Cocuzza 2003). These species may have diverged recently from a common ancestor as a result of differences in the habitats of their respective host plants. The genus *Pimpinella* is typical of herb-rich areas and



**Figure 2c.** MrBayes tree estimated using 648 bp at the 3' end of COI for selected *Anuraphis* species.

wooded pastures, whereas *O. chironium* prefers uncultivated dry land with a Mediterranean climate (Pignatti 1982). The phenomenon of host-races as a first step leading to speciation has been repeatedly observed in phytophagous insects (Drès and Mallet 2001) and is common in aphids (Sunnucks et al. 1997; Margaritopoulos et al. 2007), especially in populations that have partially or totally lost the sexual generation in favour of continuous parthenogenetic reproduction. Host-plant use may represent a food resource niche that favours the speciation process of species in sympatry (Peccoud et al. 2010). Moreover, low genetic diversity at the COI level is typical of taxa with recent ecological divergence (Jimbo et al. 2011) and can explain the low genetic divergence (<1%) reported in some aphid groups (Footitt et al. 2008; Lee et al. 2011; Mas-simino Cocuzza and Cavalieri 2014). Lee et al. (2014) found that the COI barcode region was not helpful in the identification of 7% of the aphid species they examined. This lack of resolution could be resolved by the development of additional molecular markers with higher diversity, leading to greater accuracy in species identification (Lozier et al. 2009; Sano and Akimoto 2012; Chen et al. 2013; Lee et al. 2014). In the





**Figure 3.** Dendrogram of cluster-species results based on Mahalanobis' generalized distances in apterae for *Anuraphis* spp. (20 individual for each species) based on 16 morphometric characters (from Barbagallo and Cocuzza 2003).

The genetic results observed here in *Anuraphis* spp. closely mirror previous morphometric findings. The lack of appreciable differences in morphological characters is a phenomenon well known in various groups of aphids (Stroyan 1984; Foottit 1997; Wang et al. 2011) and this peculiarity can easily lead to the misidentification of species (Coeur d'acier et al. 2007). Because of this difficulty, there is a need for methods of investigation that can be used in conjunction with classic morphometric analysis. Confirming the finding of previous studies on aphids (Foottit et al. 2008; 2009c), the present study indicates that the COI gene may significantly aid in the correct identification of aphid species, especially in cases where morphological characters are insufficient to clarify taxonomic status. Morphometrics and the COI gene can be used in parallel to improve the discrimination of aphid species. However, an identification-integrated system that links molecular data, morphological features, life cycle, host plant, photos (in vivo and on slides) and a bibliography for each aphid species would further facilitate and improve the accuracy of aphid species determination.

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