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Interlinking journal and wiki publications through joint citation: Working examples from ZooKeys and Plazi on Species-ID

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Abstract

Scholarly publishing and citation practices have developed largely in the absence of versioned documents. The digital age requires new practices to combine the old and the new. We describe how the original published source and a versioned wiki page based on it can be reconciled and combined into a single citation reference. We illustrate the citation mechanism by way of practical examples focusing on journal and wiki publishing of taxon treatments. Specifically, we discuss mechanisms for permanent cross-linking between the static original publication and the dynamic, versioned wiki, as well as for automated export of journal content to the wiki, to reduce the workload on authors, for combining the journal and the wiki citation and for integrating it with the attribution of wiki contributors.

Introduction

The static character of academic publications inherited from the era of paper publishing is obviously at odds with the dynamic and interminable process of taxonomic research (Erwin and Johnson 2000, Penev et al. 2009). The Internet has enabled online publishing methods that provide straightforward ways to change published content over time. On the other side, time-stamped, non-modifiable, persistent scientific publications are one of the fundamentals of scholarly communication and publishing practices. They are important for several reasons, most importantly for a permanent publication record, citability and compliance with the biological Codes, e.g., The International Code of Botanical Nomenclature (ICBN) and The International Code of Zoological Nomenclature (ICZN). They also provide a stable publication record for any other purpose, e.g., registration of priority and academic credit, scientific trust, assessment of priority for ideas as well as for taxon descriptions, management of publication records and bibliographic indexing. Many online publication systems guarantee neither persistence nor a public traceability of version changes over time.

The idea of a combination between journal-published taxon descriptions and Internet-based updates was first proposed by Erwin and Johnson (2000) at a time when wikis were niche applications known only to few. The wiki approach was rendered popular by Wikipedia; the MediaWiki software it runs on is an environment in which users can create and edit public content. Importantly, wiki software like MediaWiki keeps a publicly accessible, time-stamped history of all changes over time, which renders it interesting from the perspective of scholarly peer review (Black 2008). Nevertheless, the worlds of scholarly publishing and wikis still exhibit little overlap, despite numerous scholars contributing to both (Page 2010) and even non-academic wikis, such as Wikipedia and Citizendium, that actively invite expert contributions (The Guardian 2011, Morris and Mietchen 2010).

In an attempt to reconcile the static character of taxon descriptions and the need to continuously update them, ZooKeys published recently the pilot article of Hendriks and Balke (2011), where the journal description of the new beetle species *Neobidessodes darwiniensis* was exported manually to a wiki taxon page on species-id.net on the day of publication (http://species-id.net/wiki/Neobidessodes_darwiniensis). The original journal description contains the link to the wiki page of the species, while the wiki page points to the journal publication as original source of information. Both sides will profit from such a workflow: the wiki version of the description can be further edited and expanded with new information, providing an opportunity for a potentially eternal process of improvement and data enrichment; at the same time, the journal publication validates taxa (re-)descriptions and provides a permanent publication record. The presence of the originally published source on the wiki page derived from it and the explicit requirement to cite both, will increase citation rates of taxonomic publications (see, e.g., Nielsen 2008). Low citation rates have been recognized as one of the main impediments to contemporary taxonomy (Werner 2006, Agnarsson and Kuntner 2007).

The current paper describes an improved method to (1) combine the citation of the original taxon treatment published in a journal with the versioned wiki page of it into a single bibliographic reference; (2) list the names of the contributors to the particular versioned wiki page in the same reference alongside with the date and version number; (3) automatically export taxon treatments and create wiki pages of them simultaneously with the journal publication; (4) provide a permanent cross-linking between the original publication and the respective versioned wiki pages.

The method is demonstrated by way of sample papers (Stoev and Enghoff 2011, Bantaowong et al. 2011) published in this issue. The papers serve as an example of journal publication of taxon treatments (of both newly described and redescribed taxa) that are automatically exported to wiki (species-id.net) on the day of publication. Treatments from any paper published as TaxPub XML file can easily be uploaded, too, and we illustrate that with two PhytoKeys articles published in 2010 (Kress et al. 2010, Knapp 2010). Further, we illustrate how taxon treatments from legacy literature can be exported from Plazi's treatment repository to Species-ID. A list of the Species-ID taxon pages generated in the frame of the present project is given in Appendix 1.

Citation of versioned documents

Currently, wiki pages like other Internet resources are usually cited as URLs, often adding a "date of accession". Clearly, the latter has little practical meaning if the cited Internet resource does not provide a public version history. On most wiki platforms, however, each separate edit of a wiki page is versioned and time-stamped in a publicly accessible manner. This feature, along with the ease with which edits can be made, is a major factor contributing to the phenomenal success of Wikipedia and the high popularity of wiki environments in general.

Any versioned online source, however, has the problem that two or more possible citations (and corresponding URLs) might exist, that is, the one for the most recent version and the one or more for previous versions in time. For many use cases, it is desirable to link to the most recent, presumably improved or error-corrected URL, and thus this URL is normally used when referring to an article. At arXiv and Nature Precedings, for instance, the generic identifier always points to the latest version (cf. http://arxiv.org/abs/1103.3216 and http://dx.doi.org/10.1038/npre.2009.3267), even though individual versions can technically be cited as easily (cf. http://arxiv.org/abs/1103.3216v2 and http://dx.doi.org/10.1038/npre.2009.3267.4). Both sites explain the versioning in places where few citing authors will look, which makes it difficult to establish a consistent citation pattern for different versions of the same article. Similarly, the "permanent link" available for any version of any page in a standard wiki environment (cf. Fig. 1) is not known to all users who cite wiki articles. Furthermore, attribution to the contributors to a versioned wiki page provides another barrier to a proper citation, because it requires significant wiki experience and substantial work to extract the names of the contributors from a highly edited page.

Lack of appropriate mechanisms for recognition of wiki authorship is one of the major reasons for many academics to stay away from the wiki world (cf. George 2007, Prug 2010). Clear attribution of wiki authorship is an important prerequisite for receiving credit. Thus, wiki pages intended to be cited in a scholarly manner would certainly benefit from an on-page display of a recommended citation format. In cases where the entire content has been created in an on-wiki collaboration, this is just a technical problem, for which several solutions exist (e.g., Suh et al. 2008). However, in the example of a close journal-to-wiki workflow, the first version of a page is near-identically derived from a source outside the wiki. The challenge is how to properly cite both the first, original version and the later on-wiki contributions in a single and consistent way.

Thus far, wiki elements in scholarly publishing are rare (for an overview, see Mietchen et al. 2011). In the life sciences, the two most prominent examples are RNA Biology and Scholarpedia. RNA Biology requires authors to submit the draft for a Wikipedia article along with certain types of manuscript submissions. The Wikipedia draft article is included in the peer review process and its generic wiki address (e.g., http://en.wikipedia.org/wiki/SmY, meanwhile changed to http://en.wikipedia.org/wiki/SmY_RNA) mentioned in the journal article (i.e. Jones et al. 2009), which in turn is then cited from the Wikipedia article once the journal article has been published. This way, the journal and wiki versions are interlinked yet cited independently. Scholarpedia is a review journal implemented entirely on MediaWiki. For all its accepted articles (e.g., Dawson and Lauterbur 2008), it always clearly displays the generic wiki address (i.e., http://www.scholarpedia.org/article/Magnetic_resonance_imaging), the DOI and the wiki revision number (the current one is #73087), states a recommended citation at the bottom of the page – Joan Dawson, Paul C. Lauterbur (2008) Magnetic resonance imaging. Scholarpedia, 3(7): 3381, (go to the first approved version) – and provides a prominent link on the top right to an auxiliary page containing the citation in standard bibliographic formats.

To the best of our knowledge, however, there is no established citation format that combines both an original non-wiki source and the respective wiki page within one and the same citation reference. In our understanding, such a mechanism should credit both the authors of the original publication and the contributors to the respective version of the wiki page. In addition, the reader will always be referred to a defined, numbered and time-stamped version of the wiki page that also links directly to the original published source of the wiki content.

We propose to cite wiki pages based on original scholarly publications according to the following scheme:

> <Author 1, Author 2 ..... Author n> (<year>) <Title> <Journal> <IssueNo> <pages> <DOI>. *Versioned wiki page:* <YEAR-MM-DD>, version <sequential number of revision>, http://species-id.net/wiki/index.php?title=Genus_species&oldid=<sequential number of revision>, contributors (alphabetical order): Contributor 1, Contributor 2 ..... Contributor N.

The citation style is automatically added to the top of each page on Species-ID by means of a template, as illustrated in Fig. 1.

The features of the proposed citation mechanism are outlined below:

1. The citation of both the original publication and the wiki page is embedded in the automated export to the wiki.
2. The names of contributors are automatically extracted from the page history and displayed on the versioned wiki page that a user is viewing. This list includes only users who contributed to the currently displayed version of the wiki page, as well as those who have contributed to all earlier versions.
3. The version number is unique within the respective wiki (it is a consecutive revision number for all revisions of all pages on the same wiki).
4. The date field lists the date of creation of the respective version (the date when the page has been accessed is available separately).
5. The "page history" link allows a quick overview of all revisions made on the paper, usually listing also the respective time stamp and author, along with a short summary of the revision.
6. Furthermore, as a service to the reader, ready-to-copy citations in BibTeX, RIS (Endnote) and wiki (Wikipedia, Citizendium) formats are provided, and supplementary formats can easily be added in.

Furthermore, this way of citation could be applied not only to recent publications but also to historical literature from where original taxa descriptions could be extracted, marked up and exported to the wiki for further updates, as shown in the examples from Plazi (Figs 3, 4).

Automated export to a wiki

Pensoft routinely publishes XML versions of the journal papers based on the TaxPub extension of the NLM DTD (National Library of Medicine's Document Type Definitions format) (Catapano 2010). The XML-based markup process is embedded in the editorial practice of Pensoft (see Penev et al. 2010) and permits the tagged content to be fragmented in a way that separate parts of an article can be exported, alongside with the relevant citation metadata, onto various platforms, for example Encyclopedia of Life (EOL), the Global Biodiversity Information Facility (GBIF), Plazi and Species-ID. The XML-tagged text also provides the basis for several kinds of semantic enhancements to the published text to facilitate reading, internal cross-linking and external links (Shotton 2009, Penev et al. 2010).

To automate the export to a wiki environment, in this case Species-ID, we developed a tool, named Pensoft Wiki Convertor (PWC), which converts the XML versions of the papers into MediaWiki-based wiki pages. The PWC also converts the internal structure of taxon treatments (e.g., Type Location, Description, Distribution, Etymology and others) into sections of the wiki page. In addition, it converts reference lists and identification keys, exports taxon images and places them on the wiki page. At the same time, the PWC uses several wiki templates to facilitate the display of recommended citations, taxonomic classifications and other content elements in a way that is consistent across the site and easily editable as well. Several of the hyperlinks present on

Sinocallipus catba

Notice: The first version of this taxon page is derived from the original publication and was created by Pensoft Publishers on behalf of the original author(s), who should always be credited. Further contributors may edit and improve the content of this taxon page and, consequently, need to be credited as well (see page history). Any assessment of factual correctness requires a careful review of the original article as well as of subsequent contributions.

If you are uncertain whether your planned contribution is correct or not, we suggest that you use the associated discussion page instead of editing the taxon page directly.

This page should be cited as follows:
Stoev P, Enghoff H (2011) A review of the millipede genus *Sinocallipus* Zhang, 1993 (Diplopoda, Callipodida, Sinocallipodidae), with notes on gonopods monotony vs. peripheral diversity in millipedes. ZooKeys 90: 13–34, doi: 10.3897/zookeys.90.1291. *Versioned wiki page*: 2011-04-14, version 4534, http://species-id.net/w/index.php?title=Sinocallipus_catba&oldid=4534, contributors (alphabetical order): ZooKeys.

Citation formats to copy and paste
[Expand]

Taxonavigation

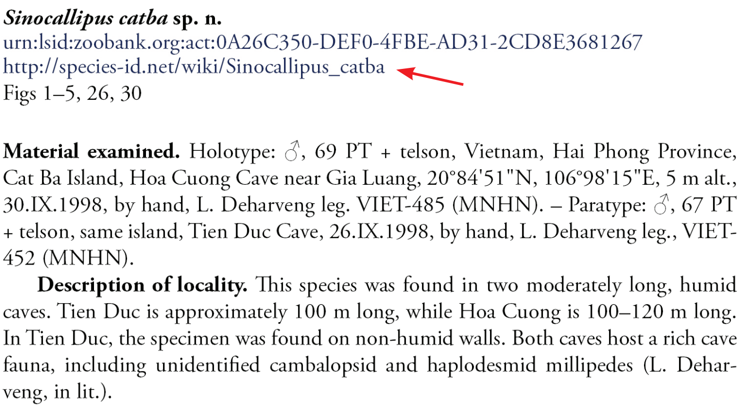
Ordo: Callipodida
Familia: Sinocallipodidae
Genus: Sinocallipus

Name

- *Sinocallipus catba* Stoev & Enghoff, 2011 – Wikispecies link – ZooBank link – Pensoft Profile

This page should be cited as follows:
Stoev P, Enghoff H (2011) A review of the millipede genus *Sinocallipus* Zhang, 1993 (Diplopoda, Callipodida, Sinocallipodidae), with notes on gonopods monotony vs. peripheral diversity in millipedes. ZooKeys 90: 13–34, doi: 10.3897/zookeys.90.1291. *Versioned wiki page*: 2011-04-14, version 4534, http://species-id.net/w/index.php?title=Sinocallipus_catba&oldid=4534, contributors (alphabetical order): ZooKeys.

Figure 1. Citation template for the simultaneous journal and wiki publication of *Sinocallipus catba* Stoev & Enghoff, 2011 (generic link: http://species-id.net/wiki/Sinocallipus_catba, permanent link of the version depicted in the figure: http://species-id.net/w/index.php?title=Sinocallipus_catba&oldid=4534). The generic link always points to the most recent version of the page, while a permanent link is specific to one particular revision.



***Sinocallipus catba* sp. n.**
urn:lsid:zoobank.org:act:0A26C350-DEF0-4FBE-AD31-2CD8E3681267
http://species-id.net/wiki/Sinocallipus_catba
Figs 1–5, 26, 30

Material examined. Holotype: ♂, 69 PT + telson, Vietnam, Hai Phong Province, Cat Ba Island, Hoa Cuong Cave near Gia Luang, 20°84'51"N, 106°98'15"E, 5 m alt., 30.IX.1998, by hand, L. Deharveng leg. VIET-485 (MNHN). – Paratype: ♂, 67 PT + telson, same island, Tien Duc Cave, 26.IX.1998, by hand, L. Deharveng leg., VIET-452 (MNHN).

Description of locality. This species was found in two moderately long, humid caves. Tien Duc is approximately 100 m long, while Hoa Cuong is 100–120 m long. In Tien Duc, the specimen was found on non-humid walls. Both caves host a rich cave fauna, including unidentified cambalopsid and haplodesmid millipedes (L. Deharveng, in lit.).

Figure 2. The original description of *Sinocallipus catba* Stoev & Enghoff, 2011 displaying the generic URL of the wiki page (http://species-id.net/wiki/Sinocallipus_catba) right below the ZooBank LSID (see arrow).

the ZooKeys article – e.g., ZooBank LSIDs, georeferenced coordinates and others – are also transferred to and displayed on the wiki page.

Conversely, the hyperlinked URL of the generic wiki page for each taxon treatment is published in the original journal publication, right next to the taxon treatment name (Fig. 2).

GoldenGATE Search & Retrieval Server by Guido Sautter, IPD Böhm, Universität Karlsruhe (TH), 2009
Search through 12842 treatments (605 documents) in the archive. view statistics

Anochetus boltoni Fisher

Publication Data, Additional Information (status, external links, etc)

citation of original description	Fisher, B. L. & Smith, M. A., 2008, A revision of Malagasy species of Anochetus Mayr and Odontomachus Latreille (Hymenoptera: Formicidae)., PlosOne (3), pp. 1-23: 4-6
publication ID	21401
link to original citation	http://hdl.handle.net/10199/15447
additional text versions	Plain XML TaxonX
scientific name	Anochetus boltoni Fisher
status	sp. nov.
description page, figures	
external databases	Antweb Page ZBK HNS Edit treatment
distribution map	GoogleMaps

Treatment

Anochetus boltoni Fisher ZBK HNS sp. nov.

urn:lsid:zoobank.org:act:B6C072CF-1CA6-40C7-8396- 534E91EF7FBB Figures: worker 2a,b, 5a; male 2c,d, 8a; map 6a

Type Material: Holotype worker, MADAGASCAR: Antsiranana, Parc National de Marojejy, Manantenina River, 28.0 km38° NE Andapa, 8.2 km 333° NNW Manantenina, 14°26'12"S, 049°46'30"E, 450 m, sifted litter, rainforest, 12-15

Figure 3. Treatment of *Anochetus boltoni* Fisher extracted through XML markup from the original paper of Fisher and Smith (2008) and deposited at the Plazi Treatment Repository (www.plazi.org).

Anochetus boltoni

Notice: The first version of this taxon page is derived from the original publication, whose author(s) should always be credited. Further contributors may edit and improve the content of this taxon page and, consequently, need to be credited as well (see page history). Any assessment of factual correctness requires a careful review of the original article as well as of subsequent contributions.

If you are uncertain whether your planned contribution is correct or not, we suggest that you use the associated discussion page instead of editing the taxon page directly.

This page should be cited as follows:
Fisher, B. L., Smith, M. A. (2008) A revision of Malagasy species of Anochetus Mayr and Odontomachus Latreille (Hymenoptera: Formicidae). PLoS ONE 3 : 4 – 6, doi: 10.1371/journal.pone.0001787. *Versioned wiki page:* 2011-04-14, version 4422, http://species-id.net/w/index.php?title=Anochetus_boltoni&oldid=4422 , contributors (alphabetical order): Daniel Mietchen, PlaziBot.

Citation formats to copy and paste [Expand]

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Taxonavigation

Genus: Anochetus

Name [edit]

Anochetus boltoni Fisher, B. L., 2008 – Wikispecies link – ZooBank link – Pensoft Profile

- *Anochetus boltoni* Fisher, B. L., 2008, PLoS ONE 3: 4-6.

Distribution

Distribution and biology. The distribution is limited to collections made between 450 m and 750 m in rainforest in Parc National de Marojejy and 240 m from Ambanitaza near Antalaha (Fig. 4a). It has been collected three times in rotten logs and once in a leaf litter sample. Males have been collected in malaise samples on 20-25 Dec 2004 at 488 m in Parc National de Marojejy CO1. The two populations where collections have been made to date are characterized by a deep divergence within the DNA barcode region (Maximum - 8%) (Fig. 15).

Figure 4. Wiki page of *Anochetus boltoni* Fisher (http://species-id.net/wiki/Anochetus_boltoni) exported from the Plazi Treatment Repository to Species-ID.

Additional wiki templates embedded by the PWC provide various links of the taxon name to external biodiversity resources (e.g., GBIF, EOL, NCBI, PubMed, Biodiversity Heritage Library (BHL), ZooBank, the International Plant Name Index (IPNI), Index Fungorum, Tropicos, PLANTS, Wikispecies, Wikipedia and others) harvested "on the fly" through the Pensoft Taxon Profile (PTP) tool.

Once the XML file of a paper is converted into MediaWiki markup, the PWC uses wiki bots to automatically create separate wiki pages for each taxon treatment and to upload the respective content there.

The Species-ID wiki

Species-ID (http://species-id.net) is dedicated to collecting and integrating open taxon descriptions and identification tools for different taxa. The audience addressed are scientists and naturalists, both amateurs (Pearson et al. 2011) and professionals. The huge task of providing adequate documentation of the world's biota requires a collaborative approach. The project is presently in an initial phase. Nonetheless, it already provides a sufficient infrastructure and sample pages to illustrate its mission.

A successful wiki platform can exist and develop only if there is an active community contributing to it. Several layers of contributions are welcome to Species-ID:

- Descriptions and identification tools (species treatments, dichotomous, polytomous, multi-access keys, etc.).
- Checking, editing and updating of existing wiki pages.
- Enhancing the access and usability through restructuring, categorizing, semantic wiki information or tools, wiki templates or adding new software extensions.

Species-ID publishes materials under an open content policy that is compatible with other open content projects such as Wikipedia or Open educational resources (OER). It does not resort to the "non-commercial" clause (which is highly problematic and not an open source license, see Hagedorn 2011). Unlike Wikipedia, which is dedicated to summarizing information previously published elsewhere, original and authored information may be published on Species-ID. Despite this policy, for major revisions and all nomenclatural acts, a publication in a journal is recommended. Many smaller contributions, insights, and other modifications, however, may not warrant a journal publication and are welcome on Species-ID directly. The submission of raw data files for interactive identification keys (e. g. in DELTA, Xper, SDD, or other formats) is especially encouraged to provide options for a future re-use of data.

The ability to publish independent research implies the possibility of conflict. Contributions on Species-ID may therefore either be shared, normal pages which are dedicated to neutrality, or authored pages (having the authors' names in the title), which may support the views of the respective authors in polite discourse.

Export of taxon treatments from legacy literature

Mark up and digitization of historical literature is a widely discussed problem in taxonomy (Agosti 2006, Agosti and Egloff 2009). The main goal of such initiatives is to bring taxonomic information published on paper to a new life and to re-use it through scanning, tagging and indexing technologies, so that it becomes fully searchable and retrievable by machines.

There are two working groups that already provide methods and tools for mark up of taxonomy literature: Plazi (based on the taxonX XML schema, see http://sourceforge.net/projects/taxonx and Sautter et al. 2007) and Inotaxa (based on the taXMLit schema, see Weitzman and Lyal 2007). Plazi has an organised taxon treatment repository and maintains it at www.plazi.org, alongside of associated services for dissemination of the published treatments.

Using an exporting tool similar to the PWC, Plazi provided several sample treatments on species-id.net (Appendix 1). In this way, treatments from the historical literature that are available in the Plazi repository (Fig. 3) could be opened up for updating and editing, bearing at the same time the original citation details on the wiki page (Fig. 4).

Conclusions

The present paper describes a workflow that will positively affect the exposition and dissemination of taxonomic information through:

1. Reconciliation of "static" and "dynamic" versions of a published treatment on a dedicated wiki page hosted on species-id.net;
2. Increasing exposition, discovery and linking of published information in an additional and important Internet environment, MediaWiki;
3. Combination of citation for both the original source and derivative wiki pages into a single reference record;
4. Provision of attribution to both the author(s) of the original publication and the contributor(s) to the versioned wiki page;
5. Possibility to update and edit treatments on wiki, which should provide a continuous accumulation of new knowledge;
6. Newly published and legacy treatments will be brought together to a common format for further editing, updates and possibly mashups;
7. Automating the upload to wiki will facilitate a large scale accumulation of treatments on species-id.net.
8. Wiki treatments can easily be transferred to other wikis, e.g., to Wikipedia.

We are convinced that the proposed approach will also positively influence the process of opening up data and knowledge in biodiversity science.

Acknowledgments

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Appendix 1.

List of the Species-ID pages generated automatically from the original source for the purposes of the pilot project described here.

Source: Stoev and Enghoff 2011
http://species-id.net/wiki/Sinocallipus
http://species-id.net/wiki/Sinocallipus_catba
http://species-id.net/wiki/Sinocallipus_deharvengi
http://species-id.net/wiki/Sinocallipus_jaegeri
http://species-id.net/wiki/Sinocallipus_simplipodicus
http://species-id.net/wiki/Sinocallipus_steineri
http://species-id.net/wiki/Sinocallipus_thai

Source: Bantaowong et al. 2011
http://species-id.net/wiki/Amynthas_phatubensis
http://species-id.net/wiki/Amynthas_tontong
http://species-id.net/wiki/Amynthas_borealis
http://species-id.net/wiki/Amynthas_srinan

Source: Kress et al. 2010
http://species-id.net/wiki/Larsenianthus
http://species-id.net/wiki/Larsenianthus_wardianus
http://species-id.net/wiki/Larsenianthus_careyanus
http://species-id.net/wiki/Larsenianthus_assamensis
http://species-id.net/wiki/Larsenianthus_arunachalensis

Source: Knapp 2010
http://species-id.net/wiki/Solanum_kulliwaita
http://species-id.net/wiki/Solanum_dillonii
http://species-id.net/wiki/Solanum_oxapampense
http://species-id.net/wiki/Solanum_verecundum

Source: Plazi Treatment Repository
http://species-id.net/wiki/Nixonia_masneri
http://species-id.net/wiki/Anochetus_boltoni
http://species-id.net/wiki/Formica_herculeana
http://species-id.net/wiki/Camponotus_imitator
http://species-id.net/wiki/Chromis_abyssus
http://species-id.net/wiki/Phrynoponera_pulchella

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RESEARCH ARTICLE

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A review of the millipede genus *Sinocallipus* Zhang, 1993 (Diplopoda, Callipodida, Sinocallipodidae), with notes on gonopods monotony *vs.* peripheral diversity in millipedes

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Abstract

The millipede genus *Sinocallipus* is reviewed, with four new cave-dwelling species, *S. catba*, *S. deharvengi*, *S. jaegeri* and *S. steineri*, being described from caves in Laos and Vietnam. With the new records the number of species in the genus reaches six and the genus range is extended to Central Vietnam and North and Central Laos. Both, *S. jaegeri* from Khammouan Province in Laos and *S. simplipodicus* Zhang, 1993 from Yunnan, China, show high level of reduction of eyes, which has not been recorded in other Callipodida. Peripheral characters such as the relative lengths of antennomeres, the number of ocelli, the number of pleurotergites or even the shape of paraprocts and the coloration seem to provide more information for the distinction of the species than do the relatively uniform gonopods. The differences in gonopods mainly concern the shape and length of cannula, the length and shape of coxal processes *g* and *k*, and the number of the acicular projections of the femoroid. An explanation is offered for the function of the trochanteral lobe of 9th leg-pair. It provides mechanical support for the cannula and seems to assist sperm charge and insemination during copulation. An identification key to the species in the genus is produced to accommodate the new species. The new species descriptions were automatically exported at the time of publication to a wiki (www.species-id.net) through a specially designed software tool, the Pensoft Wiki Convertor (PWC), implemented here for the first time together with a newly proposed citation mechanism for simultaneous journal/wiki publications.

Keywords

Sinocallipus, functional anatomy, gonopod monotony, troglomorphism, caves, southeast Asia, identification key, Pensoft Wiki Convertor

Introduction

Callipodidans are still poorly documented in Southeast Asia, with only 15 species, four genera and three families being hitherto known in the region (Stoev et al. 2008). The family Paracortinidae Wang & Zhang, 1993 is richest in species and includes two genera, *Paracortina* Wang & Zhang, 1993 and *Angulifemur* Zhang, 1997, and 12 species ranging from the southern Chinese provinces Yunnan, Sichuan and Tibet in the North to the provinces Thanh Hoa and Hoa Binh in Vietnam to the South (Wang and Zhang 1993, Zhang 1997, Shear 2000, Stoev and Geoffroy 2004, Stoev et al. 2008). Being very obscurely diagnosed, *Angulifemur* will most likely be synonymised with *Paracortina* when types are re-examined and further materials become available for study (Stoev et al. 2008).

The family Caspiopetalidae Lohmander, 1931, which comprises eight species distributed mainly in Central Asia, south to Punjab in Pakistan, is known in Southeast Asia with only a single cave-dwelling species, *Bollmania beroni* Stoev & Enghoff, 2005, from Yan Dong Cave in Yunnan (Stoev and Enghoff 2005). The locality lies nearly 2500 km southeast from the nearest species, *B. kohalana* (Attems, 1936) from Pakistan.

The third family, Sinocallipodidae Zhang, 1993, which is the only callipodid family entirely confined to the tropics, is considered to be the most primitive of all callipodidans and is placed in its own suborder, Sinocallipodidea (Shear 2000, Shear et al. 2003). Until now only two species of Sinocallipodidae have been described: *Sinocallipus simplipodicus* Zhang, 1993 from Xiao Cave in China, and *S. thai* Stoev, Enghoff, Panha & Fuangarworn, 2007 from the surroundings of Sri Wilai Temple, Saraburi Province, Thailand (Zhang 1993, Stoev et al. 2007). Specimens provisionally assigned to *S. simplipodicus* were recorded also from northern Vietnam (Enghoff et al. 2004) and southern Laos (Shear et al. 2003).

The biospeleological explorations of Dr Louis Deharveng and Mrs Anne Bedos (Muséum National d'Histoire Naturelle, Paris, hereafter MNHN) in caves in Vietnam, and the active collecting work of Dr Peter Jäger (Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, hereafter SMF) and Mr Helmut Steiner (Hanau, Germany) in Laos revealed new material of Callipodida which was kindly offered to us for study. All examined specimens turned out to belong to new species of *Sinocallipus*, which are described and illustrated below. In the paper we also comment on the gonopod shape in *Sinocallipus* and on some previously overlooked somatic characters, as well as the function of the trochanteral lobe on the 9th leg-pair – a structure lacking analogues in other callipodidans – in copulation. To facilitate the identification and better differentiation of the new taxa we also provide a key for their identification.

Material and methods

All material treated in the paper is preserved in 70% ethanol and is shared between the MNHN, SMF and the National Museum of Natural History, Sofia (NMNHS). All photographs were taken with a Leica DFC 420 digital camera mounted on a Leica MZ16A stereomicroscope. Automontage Pro software from Syncroscopy was used for image-stacking 3D focus expansion. Drawings were made with the aid of a camera lucida mounted on Leica-WILD M10 and Leica-MZ16 microscopes. All illustrations were processed and additionally cleaned up with Adobe Photoshop CS.

All species descriptions are automatically exported at the time of publication to a wiki platform (www.species-id.net) through a specially designed software tool, the Pensoft Wiki Convertor (PWC), implemented here for the first time and described in this issue of ZooKeys (Penev et al. 2011). The link to each taxon's wiki page is published in the paper, and vice versa, the citation of the original description is present on the top of the wiki page. The wiki environment allows a constant update of new information on the particular taxon. The citation of the wiki page includes always the original description of the taxon, along with the version number, date of creation and list of the contributors to the versioned wiki page.

Taxonomy

Genus *Sinocallipus* Zhang, 1993

urn:lsid:zoobank.org:act:F13FC586-B6EE-47D2-AC23-A8C3AD66D3C7
http://species-id.net/wiki/Sinocallipus

Sinocallipus Zhang, 1993, Proc. XI Int. Congr. Speleol. Beijing, 1993: 129. Type species: *Sinocallipus simplipodicus* Zhang, 1993, by original designation.

Emended diagnosis (based on Shear et al. 2003): A genus of moderate-size Callipodida (40–70 mm); 55–72 pleurotergites (PT); with low, narrow, primary crests; secondary and tertiary crests absent; no crest transition or setal migration; setae thin and pointed, all in an anterior position. Leg-pairs 3–11 with coxal sacs. Head of males convex, pilose, without particular modifications. Organ of Tömösváry small, inconspicuous. Hypoproct tripartite, median sclerite largest, subtrapezoidal, bearing a pair of macrosetae; lateral sclerites each with a seta emerging from the posterior margin. First and second leg-pairs visibly shorter, third leg-pair only slightly shorter than succeeding legs; tarsi undivided; with a ventral comb-like series of setae. Tarsi divided from leg-pair 4 onwards. Second leg-pair in females unmodified. Vasa deferentia opening through gonopores on small protuberances on posterior side of the second coxae. Ninth legs in males with distomedial, deeply excavated trochanteral lobe bearing pointed projections. Gonosternum extending for the entire breadth of gonopods, lying basal to gonocoxae. Gonocoxa with two medial, clavate processes (*g* and *k*) and long, slender cannula (*ca*), cannula curved or coiled; femoroid (telopodite) without prostatic groove, with 2–4 slender, narrowly separated, terminal projections directed anteromediad and overlapping or terminating close to coxal processes.

***Sinocallipus catba* sp. n.**

urn:lsid:zoobank.org:act:0A26C350-DEF0-4FBE-AD31-2CD8E3681267
http://species-id.net/wiki/Sinocallipus_catba
Figs 1–5, 26, 30

Material examined. Holotype: ♂, 69 PT + telson, Vietnam, Hai Phong Province, Cat Ba Island, Hoa Cuong Cave near Gia Luang, 20.845161°N, 106.981597°E, 5 m alt., 30.IX.1998, by hand, L. Deharveng leg. VIET-485 (MNHN). – Paratype: ♂, 67 PT + telson, same island, Tien Duc Cave, 26.IX.1998, by hand, L. Deharveng leg., VIET-452 (MNHN).

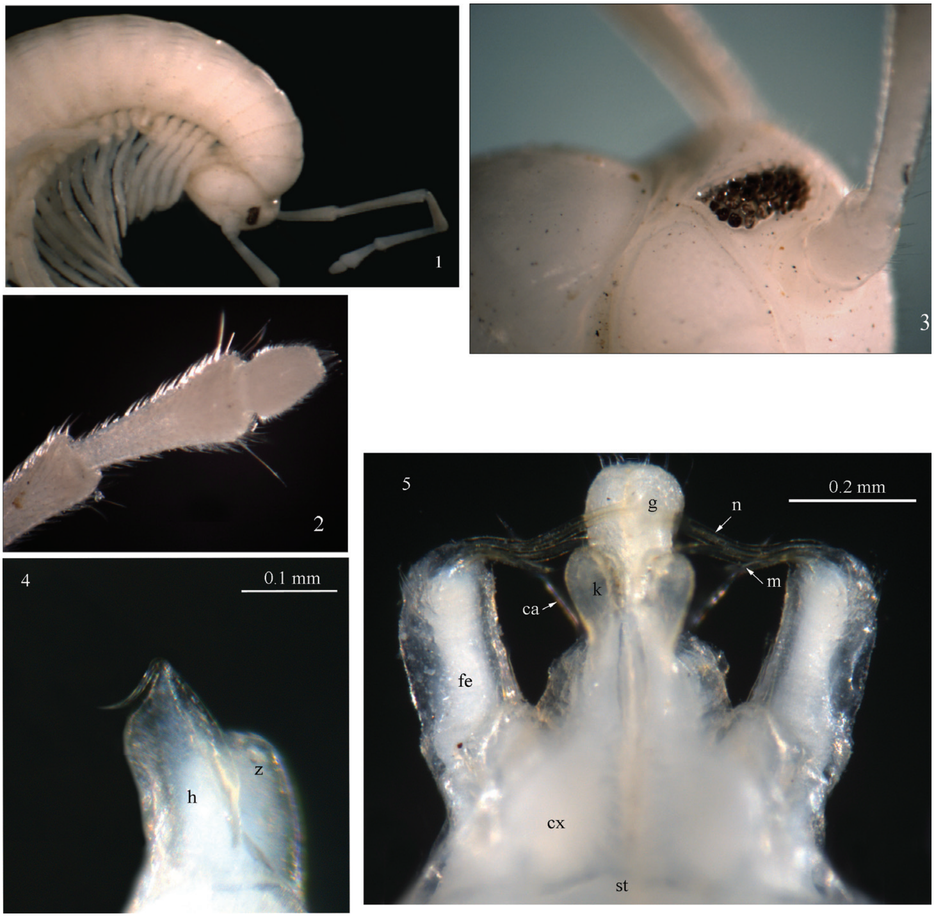
Description of locality. This species was found in two moderately long, humid caves. Tien Duc is approximately 100 m long, while Hoa Cuong is 100–120 m long. In Tien Duc, the specimen was found on non-humid walls. Both caves host a rich cave fauna, including unidentified cambalopsid and haplodesmid millipedes (L. Deharveng, in lit.).

Origin of name. For Cat Ba Island, the type locality.

Diagnosis. Differs from *S. simplipodicus*, *S. jaegeri* and *S. thai* by the white-yellowish body colour, brown antennomeres 2–5 and eye composed of 33 ocelli, and from *S. deharvengi* by the smaller body size, antennae and gonocoxal process *g*, as well as by having paraprocts divided into larger ventral and smaller dorsal sclerites.

Description. Males: Maximal length *ca* 50 mm, width of midbody PT 2.4 mm, 67–69 PT + telson. Body colour: uniformly white-yellowish, without particular coloration pattern; metazonites without posterior band. Head: uniformly white, cephalic suture visible. Antennae: long, extending beyond the posterior edge of PT 9 when folded backwards; antennomeres 2–5 light brown; 1, 6, 7 – white (Fig. 1); length of antennomeres: 1 – 0.3 mm, 2 – 1.4 mm, 3 – 1.8 mm, 4 – 1.2 mm, 5 – 1.3 mm, 6 – 0.7 mm, 7 – 0.4 mm; antennomere ratio: 3>2>5>4>6>7>1; tip of antennomere 7 with four cones protruding beyond posterior margin (Fig. 2). Eyes: black, well delineated, composed of 33 ocelli in 5 rows (Fig. 3).

Width of PT 2=3<1=4<5<6<7. PT higher than broad, ratio: 1.05 : 1. Dorsal side of collum and PT2–3 smooth, lateral sides ribbed. Crests poorly developed, broad and flattened anteriorly, abruptly narrowing and more pronounced posteriorly; 5+5



Figures 1–5. *S. catba* sp. n.: **1** head and anteriormost pleurotergites **2** tip of antenna **3** ocelli **4** trochanter of leg-pair 9 **5** gonopods, anterior view. Abbreviations: cannula (***ca***); coxa (***cx***); coxal processes ***g*** and ***k***; femoroid (***fe***); femoroidal acicular process (***n***); femoroidal subfalcate process (***m***); sternum (***st***); trochanter of leg 9: processes ***h*** and ***z***.

between the ozopores on midbody PT. Ozopores small, barely visible on most PT, lying between crests 5 and 6 in midbody PT. Paraprocts divided into smaller dorsal and larger ventral sclerites. Dorsal sclerite surmounted with two macrosetae in a vertical row. Spinnerets: long and slender, ending with a long seta.

All legs white-yellowish, long and slender, ending with a long claw. Tarsal pads very poorly developed, present on leg-pairs 3–12. No particular modifications on coxae of pregonopodal legs, prefemora of legs 4–7 swollen. Leg-pair 9 (Figs 4, 26): coxa subtrapezoidal; trochanter expanded medio-ventrad forming a rather elongated process (*h*) with a pointed tip and a smaller process *z*.

Chaetotaxy: unknown, all setae broken off.

Gonopods (Fig. 5): similar to those of congeners; coxae (*cx*): process *g* moderately large and swollen, *ca* 1.5 times the length of process *k*; processes *g* and *k* apically rounded, not truncated as in *S. jaegeri*. Femoroid (*fe*): with three slender, acicular (*n*), and one short and subfalcate (*m*) terminal projections. Cannula (*ca*): long, and slender, not coiled.

Female: unknown.

Sinocallipus deharvengi sp. n.

urn:lsid:zoobank.org:act:376E58E2-1177-4A86-9F6D-ED22C99B36AA
http://species-id.net/wiki/Sinocallipus_deharvengi
Figs 6–12, 27, 30

Material examined. Holotype: ♂, 70 PT + telson, Vietnam, Quang Binh Province, Dong Hoi, Cha Noi: Hang Cha Noi (cave), 17.641363°N 106.110375°E, 260 m alt., 8.I.1995, by hand, L. Deharveng & A. Bedos leg., VIET-064. – Paratypes: 1 juv., same locality, date and collectors; ad. ♀, 74 PT + telson, same province, Dong Hoi, Phong Nha: Hang Ruc (cave), 17.586134°N, 106.305667°E, 30 m alt., 6.I.1995, by hand, L. Deharveng & A. Bedos leg. VIET-059; 1 ♀, 70 PT + telson, same province, Dong Hoi, between Phong Nha and Cha Noi: Grotte de Troc, approx. coordinates: 17.6526°N, 106.243°E, about 70 m alt., 15.III.1997, L. Deharveng & A. Bedos leg. VIET-407 (all in MNHN).

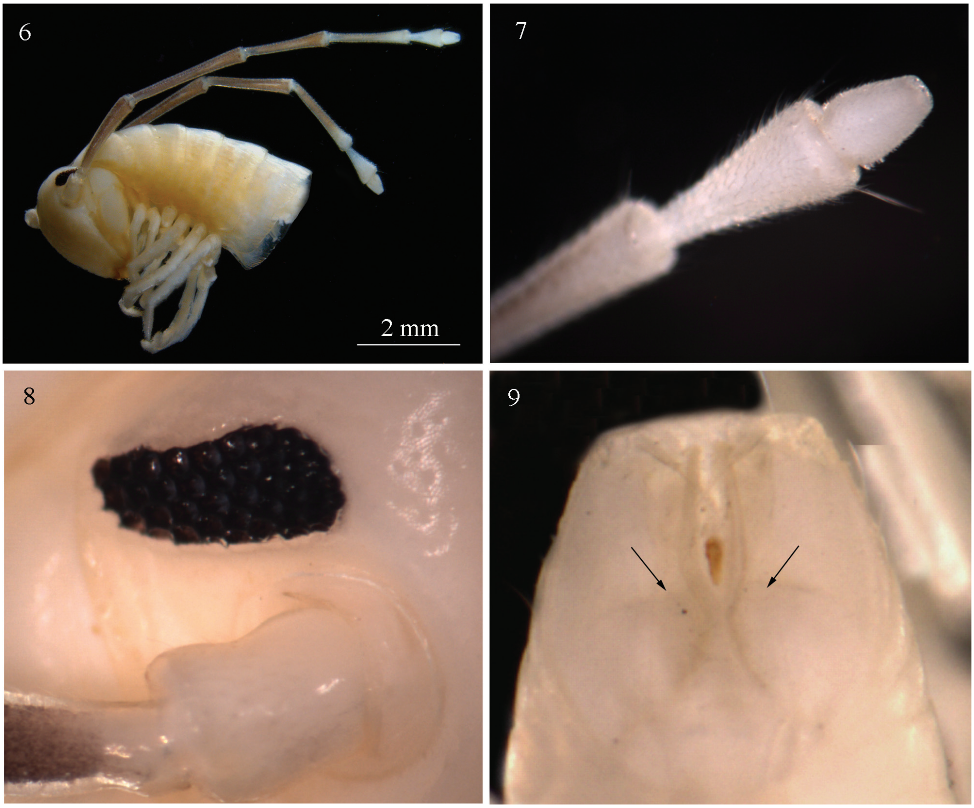
Description of locality. The species was found in several caves of moderate length (Hong Ruc about 50 m, Troc and Cha Noi more than 200 m), which seem to have never been surveyed previously. A road was built inside Hang Cha Noi during the War, and remains of rusted ammunitions were observed inside the cave at the time of collection. A rich cave fauna was found inside the Grotte de Troc, including two other species of Diplopoda, an undescribed cambalopsid, and *Eutrichodesmus asteroides* Golovatch et al., 2009 (Haplodesmidae) (Golovatch et al. 2009). All specimens were collected in the aphotic zone of the caves (L. Deharveng, in lit.).

Origin of name. Named after the French zoologist Louis Deharveng, a passionate explorer of the caves of southeastern Asia, who together with A. Bedos collected this species.

Diagnosis. Differs from congeners by having almost equally subdivided paraprocts, long antennae, strongly swollen and long gonocoxal process *g*, and comparatively short, pointed tip of the trochanteral process of leg 9. It can be distinguished from *S. simplipodicus*, *S. jaegeri* and *S. thai* also by the white-yellowish body colour and brown antennomeres 2–5, and from *S. catba* and *S. steineri* by the large body size.

Description. Males: Maximal length: *ca* 68–70 mm, width of midbody PT 3.2 mm, 70 PT + telson. Body colour: uniformly white-yellowish, without particular coloration pattern, metazonites without posterior band. Head: uniformly white, pilose; cephalic suture visible. Antennae: long, extending beyond the posterior edge of PT 10 when folded backwards; antennomeres 2–5 light brown; 1, 6, 7 – white (Fig. 6); length of antennomeres: 1 – 0.5 mm, 2 – 2.0 mm, 3 – 2.5 mm, 4 – 1.7 mm, 5 – 1.8 mm, 6 – 0.8 mm, 7 – 0.4 mm; antennomere ratio: 3>2>5>4>6>1>7; tip of antennomere 7 with four short cones (Fig. 7). Eyes: black, well delineated, composed of 37–38 ocelli in 5–6 rows (Fig. 8).

Width of PT: 1=2=3<4<5<6<7. PT higher than broad, ratio: 1.06 : 1. Dorsal side of collum and PT 2–3 smooth. Crests poorly developed, flattened, 5+5 between the



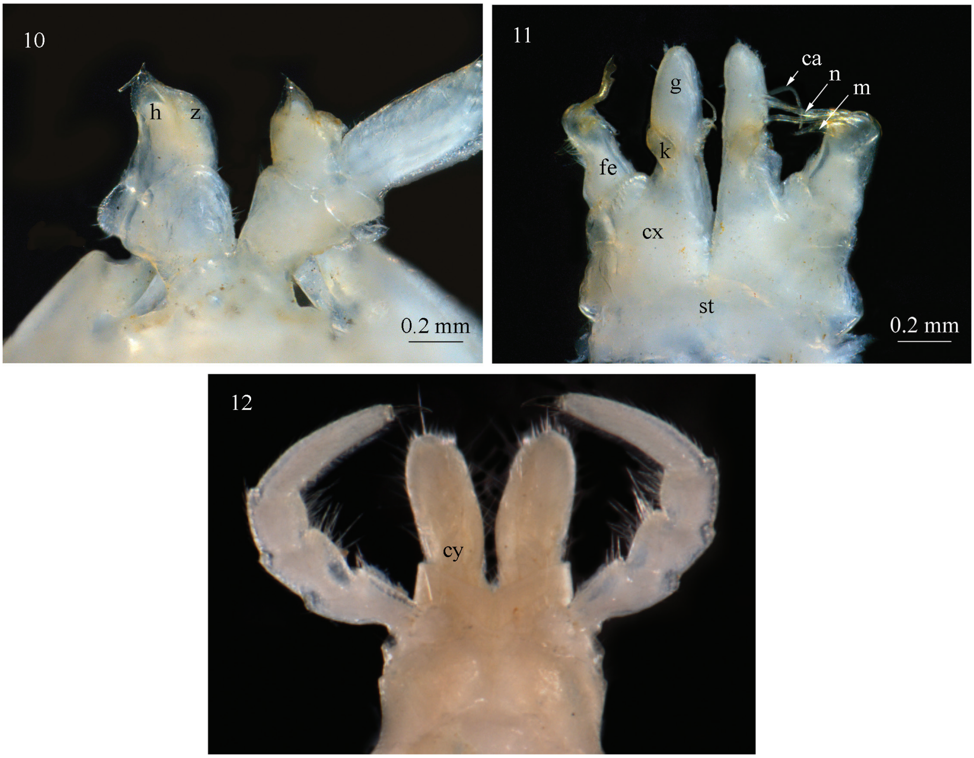
Figures 6–9. *S. deharvengi* sp. n.: **6** head and anteriormost pleurotergites **7** tip of antenna **8** ocelli **9** telson, posterior view. Arrows on Fig. 9 show the division of paraprocts.

ozopores on midbody PT, anterior part of crests broad, abruptly narrowing posteriorly. Ozopores small, barely visible on PT 5–6, lying on crest 6 in midbody PT, missing on the last 4 PT. Paraprocts divided into two almost equal-sized dorsal and ventral sclerites (Fig. 9). Dorsal sclerite surmounted by a macroseta situated on a tiny lobe. Spinnerets: long and slender, ending with a long seta. All setae on telson dark brown, contrasting with the white background.

All legs white-yellowish, long and slender, ending with a long claw. Tarsal pads very poorly developed, present on leg-pairs 3–12. No particular modifications on coxae of pregonopodal legs. Prefemora of legs 4–7 swollen. Leg-pair 9 (Figs 10, 27): coxa subtrapezoidal; trochanteral lobe (*h*) with a comparatively short tip and poorly developed process *z*.

Chaetotaxy: unknown, all setae broken off.

Gonopods (Fig. 11): similar to those of congeners; differ by the large coxal (*cx*) process *g* more than 3 times the length of process *k*; processes *g* and *k* apically rounded, not truncated as in *S. jaegeri*. Femoroid (*fe*): with three slender, acicular (*n*), and one short and subfalcate (*m*) terminal projections. Cannula (*ca*): long and slender, not coiled.



Figures 10–12. *S. deharvengi* sp. n.: **10** trochanter leg-pair 9 **11** gonopods, anterior view **12** cyphopods and leg-pair 2. Abbreviations: cannula (***ca***); coxa (***cx***); coxal processes ***g*** and ***k*** cyphopods (***cy***); femoroid (***fe***); femoroidal acicular process (***n***); femoroidal subfalcate process (***m***); sternum (***st***); trochanter of leg 9: processes ***h*** and ***z***.

Females: 70–74 PT + telson; body colour darker, lateral sides light brownish; crests more pronounced than in males; second leg-pair unmodified (Fig. 12).

***Sinocallipus jaegeri* sp. n.**

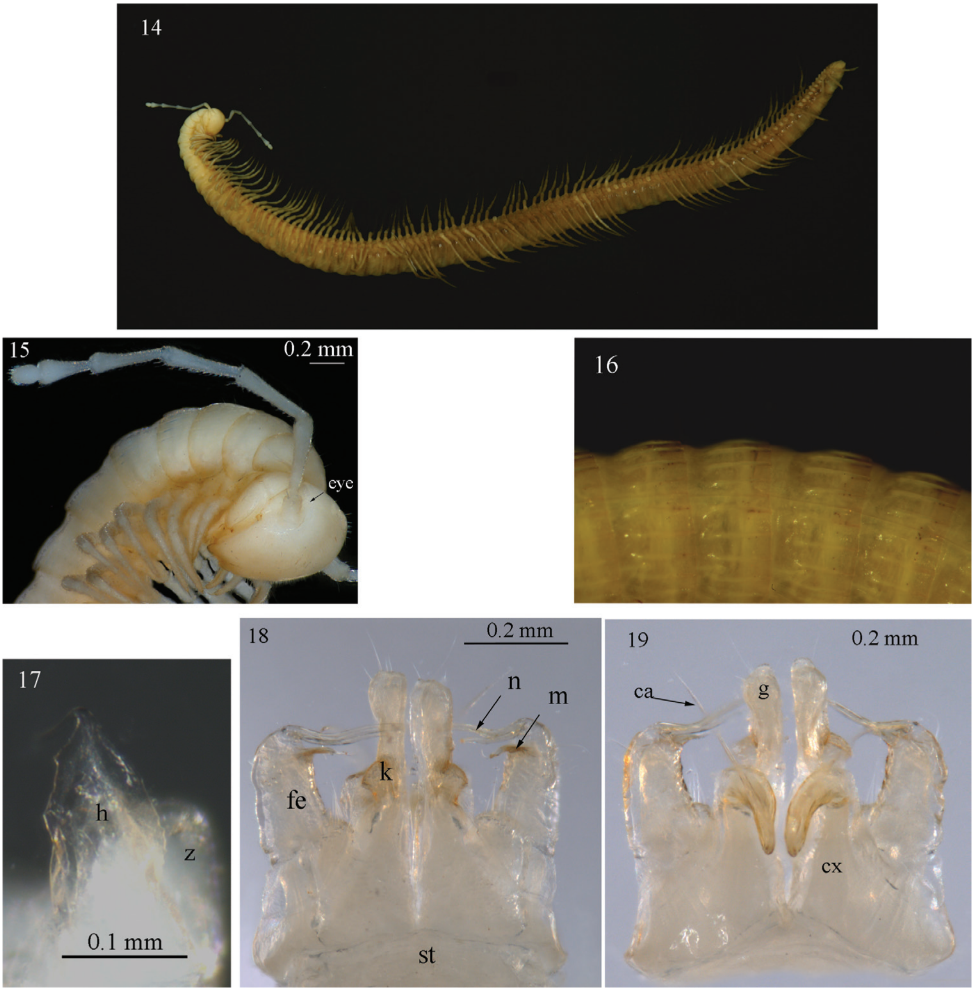
urn:lsid:zoobank.org:act:BFC1EAC4-7CB3-4391-A203-2695AE2A596C
http://species-id.net/wiki/Sinocallipus_jaegeri
Figs 14–19, 28, 30

Material examined. Holotype: ad. ♂, 61 PT + telson; length *ca* 45 mm, width *ca* 1.90 mm; Laos, Khammouan Province, 9.5 km NE Thakek, 17°26.936N, 104°52.499E, 159 m alt., in foot cave, by hand, 31.X.2004, P. Jäger & V. Vedel leg. (SMF); – Paratypes: 2 ad. ♀♀ with 58 and 59 PT, same locality as holotype, 11.III.2007, P. Jäger & F. Steinmetz leg.; ♀, 59 PT, same locality, foot cave and surrounding, 28.X.2004, P. Jäger & V. Vedel leg.; juvenile, 42 PT, same locality and collectors, 30.X.2004, P. Jäger & V. Vedel leg.; ad. ♀ broken into pieces, more than

Figure 13. View of the type locality of *S. jaegeri* sp. n. near Thakek, Laos (photo: P. Jäger).

50 PT, Khammouan Province, Thakek area, Ban Tham, 17°25.799N, 104°51.906E, 161 m alt., jungle, trees, by hand, 31.X.2004, P. Jäger & V. Vedel leg. (all in SMF; one female in NMNHS).

Description of locality. Three of the adult specimens were found in a cave situated at the foot of a limestone hill overgrown with sparse vegetation (Fig. 13). They were collected in the aphotic zone of the cave, somewhere between 30 and 80 m from the entrance. The cave is at least 100 m long, wet, with dripping water and mud on the floor and partly on the cave walls. In the cave *S. jaegeri* coexists with *Heteropoda maxima* Jäger, 2001 and *Sinopoda* sp. (Araneae: Sparassidae), *Thereuopoda longicornis* (Fabricius, 1793) (Chilopoda: Scutigeridae), and cave crickets (cf. Jäger 2007). One specimen was collected outside the cave, probably under stones close to the limestone hill, approx. 2 km SW of it where the other specimens were found.



Figures 14–19. *S. jaegeri* sp. n.: **14** habitus **15** close up of head and anteriormost pleurotergites **16** mid-body pleurotergites, dorsal view **17** trochanter of leg-pair 9 **18–19** gonopods, anterior and posterior views, respectively. Abbreviations: cannula (***ca***); coxa (***cx***); coxal processes ***g*** and ***k***; femoroid (***fe***); femoroidal acicular process (***n***); femoroidal subfalcate process (***m***); sternum (***st***); trochanter of leg 9: processes ***h*** and ***z***.

Origin of name. Named after Peter Jäger, curator of Arachnida and Myriapoda at SMF, who has been actively exploring the fauna of Laos since 2003 and collected the species.

Diagnosis. Differs from congeners by the following set of characters: reduced eyes, composed of 10–11 ocelli; well expressed, narrow, pleurotergal crests; 59–61 PT; white-yellowish body and antennae; gonopods: process *g* short, almost half length of that of *S. deharvengi*, apically truncated; *k* small and more abrupt apically than those of *S. simplipodicus*, *S. thai* and *S. deharvengi*; cannula straight.

Description. Males: Maximal length *ca* 45 mm, width of midbody PT 1.7 mm, 61 PT + telson. Body colour: white-yellowish; head and anterior 10 PT much whiter than the gray-yellowish middle and posterior ones; metazonites with a posterior light brown band, more pronounced on posterior PT (Fig. 14). Head: uniformly white, pilose, cephalic suture barely visible. Antennae: long, slightly extending beyond the posterior edge of PT10 when folded backwards; length of antennomeres: 1 – 0.4 mm, 2 – 1.2 mm, 3 – 1.5 mm, 4 – 1.0 mm, 5 – 1.0 mm, 6 – 0.6 mm, 7 – 0.3 mm; antennomere ratio: 3>2>4=5>6>1>7; tip of antennomere 7 with four cones protruding well beyond the edge. All antennomeres snow white. Eyes: very inconspicuous, transparent, in adults composed of 10–11 small ocelli in two rows (Fig. 15).

Width of PT: 2–4<1=5<6<7<8<9<10. PT higher than broad, ratio: 1.06 : 1. Dorsal side of collum and PT 2–3 smooth; complete crests series appearing from PT 4 onwards. Crests at midbody PT well apart from each other; 6+6 (lateralmost one less pronounced), no secondary crest series, all crests well expressed (ribbed), narrow, equally broad along the whole length of metazonite, not touching anteriorly (Fig. 16). Ozopores situated on midbody PT between crests 3 and 4, visible from sixth to last but two PT. Paraprocts divided into smaller dorsal and bigger ventral sclerites. Each dorsal sclerite with a pair of macrosetae situated on small lobes in vertical line. Spinnerets: long and slender, ending with a long seta each. All setae on telson dark brown, contrasting with the white background.

All legs white-yellowish, very long and slender, ending with a long claw. Tarsal pads poorly developed, present only on leg-pairs 3–12. No particular modifications on coxae of pregonopodal legs. Prefemora of posterior legs less swollen than others. Leg-pairs 4–7: coxa subquadrate; prefemur strongly swollen. Leg-pair 9 (Figs 17, 28): coxa subquadrate; trochanter with two processes: anterior one (*h*) higher, leaf-shaped, its tip very sharp, spine-like, curved cephalad; posterior process (*z*) rounded with a small hook; a small pore (*p*) opening below the hook.

Chaetotaxy (Table 1): all setae slender and apically pointed, in anterior position on all segments (excluding penultimate ones).

Gonopods (Figs 18, 19): similar to those of congeners. Coxae (*cx*): process *g* short, almost half length of that of *S. deharvengi*, apically truncated (in lateral view); *k* small and more abrupt apically than in *S. simplipodicus*, *S. thai* and *S. deharvengi*. Femoroid (*fe*): with two slender, acicular (*n*), and one shorter and subfalcate (*m*) terminal projections, latter projecting into a long and thin filament. Cannula (*ca*): long and slender, not coiled.

Females: 58–59 PT in adults; middle PT slightly broader than those of the male.

***Sinocallipus simplipodicus* Zhang, 1993**

urn:lsid:zoobank.org:act:817F9976-72F2-41A1-96C7-7A50E1A27FD4
http://species-id.net/wiki/Sinocallipus_simplipodicus
Fig. 30

Sinocallipus simplipodicus Zhang, 1993, Proc. XI Int. Congr. Speleol. Beijing, 1993: 129, figs 1–16.
Sinocallipus simplicipodus [sic!]: Wang and Mauriès 1996: 86. Shear 2000: 99.
Sinocallipus simplipodicus: Stoev et al. 2008: 7.

Table 1. Chaetotaxy of anterior PT in *S. jaegeri* sp. n.

	Anterior setae	Posterior setae
Collum	5+5	-
PT 2	5+5	-
PT 3	5+5	-
PT 4	5+5	-
PT 5	5+5	-
PT 6	5+5	-

Distribution. Only known from Xiao Cave, Hekou Yaozu Autonomous County, Yunnan Province, China.

Remarks. Although callipodidans are often found in caves, especially in Southeast Asia and southern Europe, there are no species among them possessing an eye reduction similar to that observed in *S. jaegeri* and *S. simplipodicus*. Other peripheral characters, such as the elongated antennae and legs, in addition to the apparent depigmentation, also indicate their adaptation to the underground environment. A specimen of *S. jaegeri* was found also outside caves, perhaps in deeper soil layers. The type specimens of *S. simplipodicus* which are perhaps preserved in the Institute of Zoology, Chinese Academy of Sciences, or new topotypic material need to be examined to supplement the original description of Zhang which suffers from the poor quality of its illustrations.

Sinocallipus steineri sp. n.

urn:lsid:zoobank.org:act:32886D5D-1D66-474E-B3E4-A27C7B845845
http://species-id.net/wiki/Sinocallipus_steineri
Figs 20–23, 29, 30

cf. *Sinocallipus*: Steiner 2005, p. 96.

Material examined. Holotype: ♂; 71 PT + telson, Laos, Luang Phrabang Province, Ponsai District, Ben Nambo (Thapo) Village, Tham Gia (Bat cave) (E-48-001/07), 19°57.233N, 102°25.457E, alt. approx. 400 m, 27.XII.2003, H. Steiner leg. (SMF); – Paratype: adult ♂, 67 PT, same locality, date and collector (NMNHS).

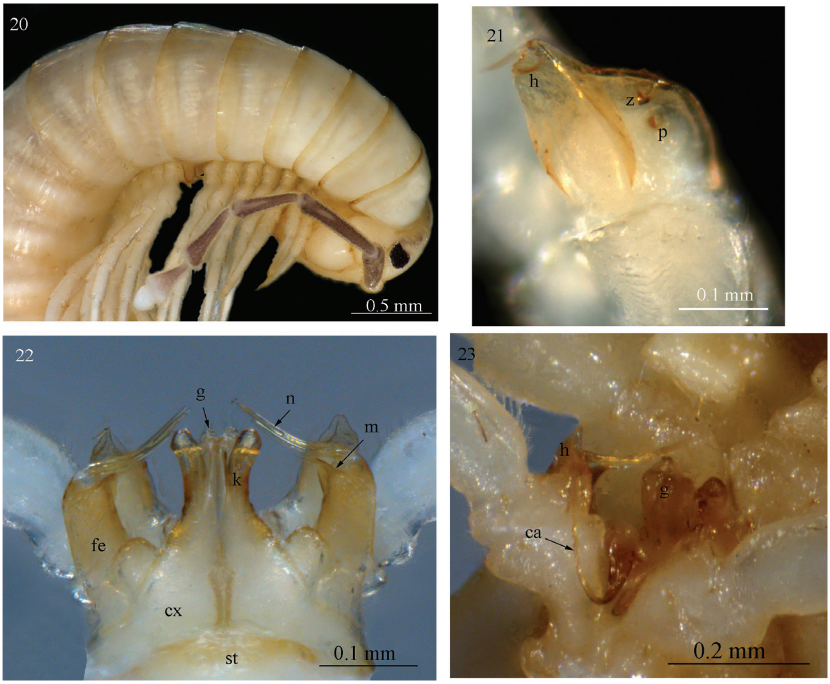
Description of locality. For detailed descriptions of the cave and its exact locality see Burgers et al. (2005). The new species has been collected from the ceiling of the cave (H. Steiner, in lit.). Cave crickets, a spider, and the centipede *Thereuopoda longicornis* co-occur with *S. steineri* (Steiner 2005, Jäger and Praxaysombath 2009).

Origin of name. Named after the German biospeleologist Helmut Steiner, an active explorer of the caves of Laos, who collected the species.

Diagnosis. Males: Differs from congeners by the following set of characters: 67–71 PT in adults; head and PT 1–4 white, remaining PT mottled light brown–grayish, antennomeres 2–6 brown; antennae moderately long, extending beyond posterior edge of PT7 when folded backwards; eyes black, well delineated, composed of 33–35 ocelli; midbody PT with 3+3 crests between ozopores; all crests flattened, almost equally broad along metazonal length, only slightly narrowed posteriorly and touching each other anteriorly. Gonopods: differ from those of congeners by the laterally narrowed gonocoxal process *g* and by the much longer process *k* being 2/3rd the height of *g*.

Description. Males: Maximal length: *ca* 54–55 mm, width of midbody PT 2.5 mm, 67–71 PT + telson. Body colour: generally white-yellowish; head and PT 1–4 white, remaining PT mottled light brown–grayish, the last 1/5 of the body brownish; metazonites with a narrow transverse posterior band. Head: white-yellowish, pilose; epicranium marbled light brown; cephalic suture visible. Antennae: moderately long, extending beyond the posterior edge of PT 7 when folded backwards; antennomeres 1 and 7 white, 2–6 – brown; length of antennomeres: 1 – 0.4 mm, 2 – 1.1 mm, 3 – 1.3 mm, 4 – 0.8 mm, 5 – 0.9 mm, 6 – 0.7 mm, 7 – 0.3 mm; antennomere ratio: 3>2>5>4>6>1>7; tip of antennomere 7 with four cones protruding well beyond the edge. Eyes: black, well delineated, composed of 33–35 ocelli in 5 rows (Fig. 20).

Width of PT: 2–3<1=4<5<6<7<8<9<10. PT slightly higher than broad; ratio: 1.07 : 1. Dorsal side of collum and PT 2–3 smooth, ribbed only laterally; complete crests series appearing from PT 4 onwards. Midbody PT with 3+3 crests between



Figures 20–23. *S. steineri* sp. n.: **20** head and anteriormost pleurotergites **21** trochanter of leg-pair 9 **22** gonopods, anterior view **23** gonopods and leg-pair 9 *in situ*, ventrocaudal view. Abbreviations: cannula (***ca***); coxa (***cx***); coxal processes ***g*** and ***k***; femoroid (***fe***); femoroidal acicular process (***n***); femoroidal subfalcate process (***m***); trochanteral pore (***p***); sternum (***st***); trochanter of leg 9: processes ***h*** and ***z***.

ozopores; no secondary crest series, all crests flattened, almost equally broad along the metazonal length, only slightly narrowed posteriorly and touching each other anteriorly. Ozopores on midbody PT lying between crests 3 and 4, visible from sixth to last but two PT. Paraprocts divided into smaller dorsal and bigger ventral sclerites. Each dorsal sclerite with a pair of macrosetae in a vertical line. Spinnerets: long and slender, ending with a long seta each. All setae on telson dark brown, contrasting with the whitish background.

All legs white-yellowish, moderately long and slender, ending with a long claw. Tarsal pads poorly developed, present only on leg-pairs 3–12. No particular modifications on coxae of pregonopodal legs. Prefemora of legs 4–7 swollen. Leg-pair 9 (Figs 21, 29): coxa subtrapezoidal; trochanter with two processes: anterior one (*h*) higher, leaf-shaped, its tip very sharpened, spine-like, curved cephalad; posterior process (*z*) rounded with a small triangular bulge; a small pore opening (*p*) below the bulge.

Chaetotaxy: pleurotergal setae barely visible, minute, one each on PT 1 and 2, others presumably broken off.

Gonopods (Figs 22, 23): similar to those of congeners, but process *k* is longer. Coxae (*cx*): process *g* laterally narrowed, not clavate as in the other congeners; apical part slighly truncated (in lateral view); *k* 2/3 the height of process g, slightly bent lateralwards at midlength; apex with a small hook pointing towards process *g*. Femoroid (*fe*): with three slender, acicular (*n*), and one shorter and subfalcate (*m*) terminal projections, latter almost half length of the longest projection. Cannula (*ca*): long and slender, not coiled, its distal part lying between processes *h* and *z* on trochanter of leg 9 in close proximity to the pore opening (*p*).

Female: unknown.

Sinocallipus thai Stoev, Enghoff, Panha & Fuangarworn, 2007

urn:lsid:zoobank.org:act:796391FA-D7CC-4701-9BB9-F4BFBF0C396A
http://species-id.net/wiki/Sinocallipus_thai
Figs 24, 30

Sinocallipus thai Stoev, Enghoff, Panha & Fuangarworn, 2007, Zootaxa 1450: p. 64, figs 1–7.
Sinocallipus thai: Stoev et al. 2008: p. 7.

Distribution. Only known from the type locality in Thailand, Saraburi Province, Muang District, Sriwilai Cave Temple, 14°41'40"N, 100°54'34"E. The unique holotype was collected under a rock at the base of a limestone hill.

Remarks. This species is easily distinguished from congeners by its strikingly snow-white anterior pleurotergites and antennal tips, contrasting with a generally dark brown body (Fig. 24). The record of *Sinocallipus* cf. *simplipodicus* from southern Laos (Shear et al. 2003) may refer to this or a morphologically similar species (Stoev et al. 2008).

Figure 24. *S. thai*: head and anteriormost pleurotergites (photo: G. Brovad).

Sinocallipus **incertae sedis**

Fig. 30

Sinocallipus cf. *simplipodicus*: Enghoff et al. 2004: 36. Vietnam, Hanoi City, 1905, leg. Dr. Boutan, coll. A. Kempf.

Sinocallipus simplipodicus: Shear et al. 2003: 9, figs 3–14. Laos, Champasak/Attapu Provinces, Dong Hua Sao National Biodiversity Conservation Area, along the Houry Phak River near the SW edge of Bolavens Plateau, 15°04'37"N, 106°10'45"E, September 1999, H. Heatwole leg.

Material examined. ad. ♀, Vietnam, Lang Son Province, Huu Lung Area, Snake cave, 19.III.1989, P. Beron leg. (NMNHS); 1 juv., same province and area, cave at 97 km N from Hanoi, 20.III.1989, P. Beron leg. (NMNHS).

Discussion

Sinocallipus is remarkable in many aspects. In addition to its apparent primitiveness compared with other callipodidans, we here focus on the lack of noticeable gonopodal variation between species and the role of the 9th male legs during copulation.

Gonopodal monotony vs. peripheral diversity

The genus *Sinocallipus* (as well as the monotypic family and suborder) can be defined by having each gonopod divided into a mesally expanded coxa bearing a cannula, and a telopodite (femoroid) without a prostatic groove bearing 2–4 acicular processes. The

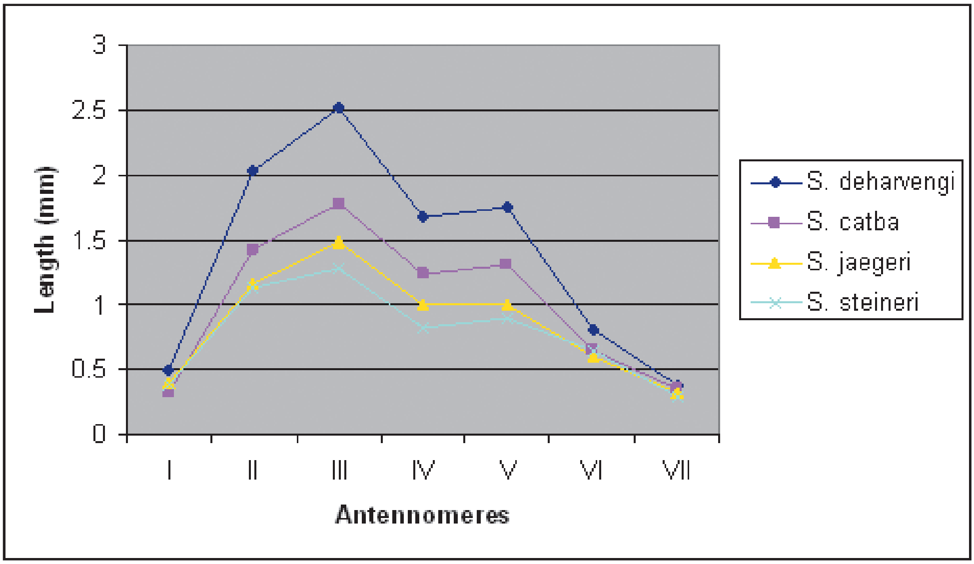


Figure 25. Graph showing antennomere lengths in the new species.

gonosternum lies at the base of the gonocoxae as in normal walking legs. In contrast to all other callipodidans which show considerable intrageneric variability in gonopod shape, gonopods in *Sinocallipus* are quite uniform. The differences mainly concern the shape and length of cannula, the length and shape of coxal processes *g* and *k*, and the number (2–4) of acicular projections of the femoroid.

In contrast, peripheral characters such as the relative lengths of antennomeres (Fig. 25), the number of ocelli, the number of pleurotergites or even the shape of paraprocts and the coloration seems to provide more information for the distinction of the species. There is a high degree of color variation in sinocallipods – from pale or light yellow-brownish in most of the species to dark brown in *S. thai* (the only known specimen of which was collected outside a cave). Body size also varies substantially, from around 40 mm in *S. simplipodicus* to more than 70 mm in *S. deharvengi*. The same is true for the length of antennae where *S. deharvengi* and *S. jaegeri* on one hand and *S.*

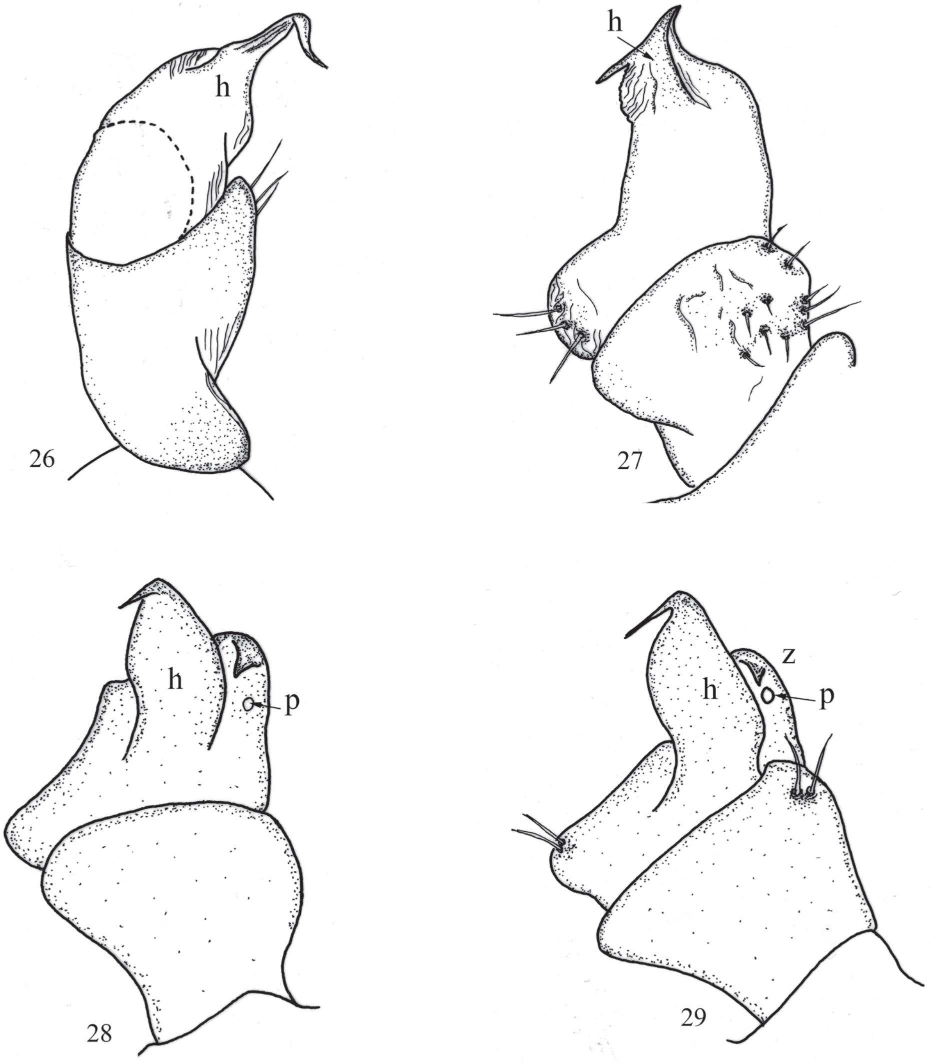
Table 2. Relative length of antennae in *Sinocallipus* species

Species	Antennae reaching back
S. catba	beyond posterior edge of PT9
S. deharvengi	beyond posterior edge of PT10
S. jaegeri	beyond posterior edge of PT10
S. simplipodicus	beyond posterior edge of PT8*
S. steineri	beyond posterior edge of PT7
S. thai	slightly beyond posterior edge of PT4

*inferred from fig. 1 in Zhang (1993).

thai on the other demonstrate the extreme cases (Table 2, Fig. 25). The shape of the trochanteral process of the 9th male leg-pair also varies and could be used as a species-specific character (Figs 26–29).

Sinocallipus thus enters the ranks of millipede groups where the gonopods – often regarded as a *sine qua non* for species distinction in millipedes – are of little use for taxonomists while non-gonopodal (”peripheral”, ”somatic”) structures provide characters for identification. Hoffman (1981) called attention to what he called ”diphasic evolution” in polydesmidan millipedes: the difference between related species lies either in the exterior morphology, with gonopods showing little diversity, or in the



Figures 26–29. 9th leg in *Sinocallipus*: **26** *S. catba* sp. n. **27** *S. deharvengi* sp. n. **28** *S. jaegeri* sp. n. **29** *S. steineri* sp. n. Abbreviations: process ***h***; process ***z***; pore (***p***).

gonopod structure, with peripheral characters showing less variation, see also Hoffman (1990). Examples of millipede groups with monotonous gonopods and diverse peripheral characters include the oxydesmid genus *Coromus* (Hoffman 1990), parts of the julid genera *Nepalmatoiulus*, *Dolichoiulus* and *Pachyiulus* (Enghoff 1987, 1992, Frederiksen, Petersen and Enghoff, unpubl.), the rhinocricid genus *Anadenobolus* (Bond and Sierwald 2002) and the harpagophorid genus *Thyropygus* (Pimvichai, Enghoff and Panha, unpubl.).

Commentary on functional anatomy of gonopods and ninth male legs in *Sinocallipus*

Shear et al. (2003) stated that the cannula must represent the functional element in *Sinocallipus* copulation. According to these authors the most plausible method of spermatophore or seminal fluid transfer seems to be directly by the cannula which, being the longest gonopodal structure, could most easily contact the openings of the vasa deferentia to be "charged," and subsequently penetrate the female cyphopods during copulation. Shear et al. (2003) found further support for this notion in the structure of telopodite which lacks a prostatic groove. However, no explanation has been offered for the function of the trochanteral lobe of 9th leg-pair – a structure lacking analogues in other callipodidans.

A close-up photograph of the gonopodal region of *S. steineri* (Fig. 23) shows the distal part of the cannula embedded in the groove formed by the trochanteral processes on leg 9 in close proximity to the pore (*p*). This suggests that the 9th legs play a role in the copulation process, provided that the interpretation of Shear et al.' is correct and indeed the cannula is the main structure used for sperm transfer. Besides mechanical support the trochanter probably provides secretions through the pore (*p*). However, until proven by direct observation, this statement remains speculative.

Other unusual morphological traits

Sinocallipus exhibits further traits which were previously unknown in Callipodida. The division of each paraproct into a smaller dorsal and a larger ventral sclerite seems in general to show no variation within the order. However, in *S. deharvengi* the paraprocts are divided exactly in the middle forming two nearly equal-sized halves (Fig. 9), while in all congeners they have the usual callipodidan shape. A character that might prove to be an autapomorphy for the genus is the presence of more than one seta (usually a pair, arranged in a vertical row) on the dorsal sclerite of each paraproct. This has been observed so far in four of the species and also in the female specimen of uncertain identity from the Snake cave, while it has not been recorded for the other species (where it might have been overlooked).

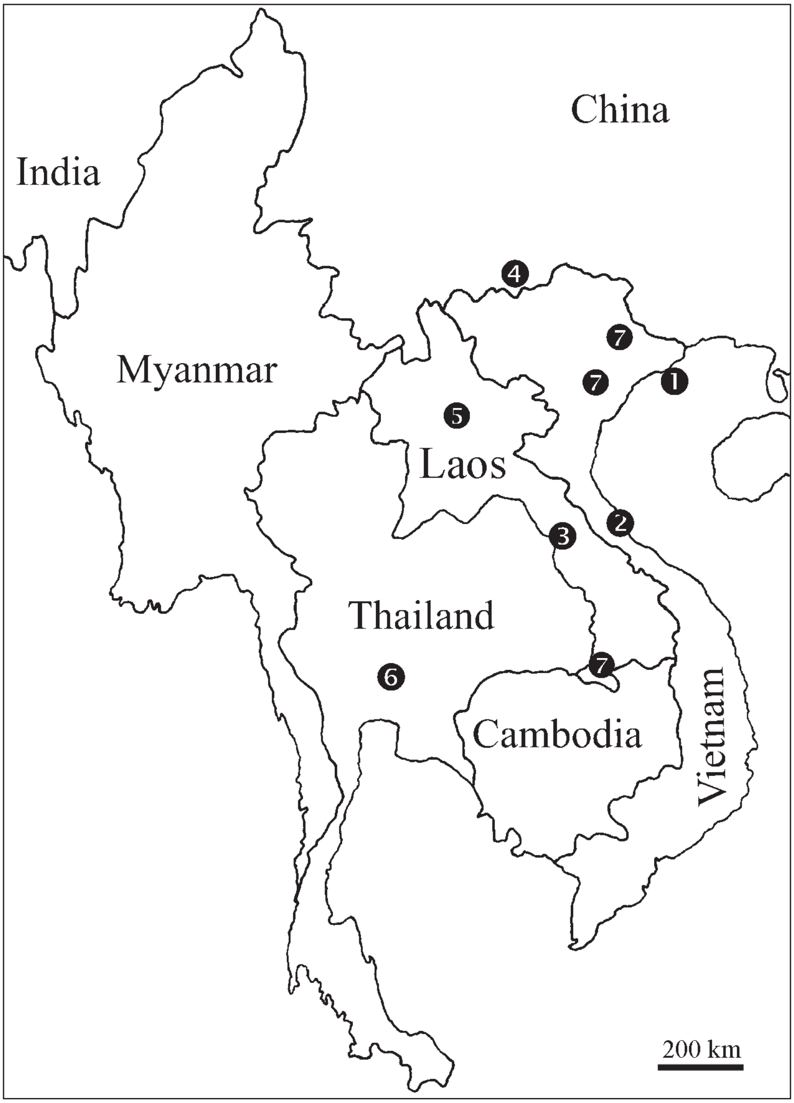


Figure 30. Distribution of the species of genus *Sinocallipus*: **1** *S. catba* sp. n. **2** *S. deharvengi* sp. n. **3** *S. jaegeri* sp. n. **4** *S. simplipodicus* **5** *S. steineri* sp. n. **6** *S. thai* **7** *Sinocallipus* spp.

Distribution

Sinocallipus is the only genus in Callipodida entirely confined to the tropics, being hitherto known only south of the Tropic of Cancer, where its species are primarily confined to limestone caves and their surroundings. At present the genus range comprises the extreme South of China in Yunnan; Lang Son, Ha Noi, Quang Binh and Hai Phong provinces in North and Central Vietnam; Saraburi Province in South Central Thailand; and Khammouan, Luang Phrabang and Champasak/Attapu provinces in Laos (Fig. 30). Shelley and Golovatch (2011) in their *magnum opus* on millipede biogeography presented updated maps of the distribution of the order Callipodida. These authors regard Callipodida as exhibiting an exclusively Laurasian distribution pattern and the occurrence of callipodidans in China and SE Asia as resulting from "spread into these areas after accretion of the "proto-southeast Asia" Gondwana I terranes". Although their explicitly not phylogeny-based narrative is not entirely clear on this point, it seems that they regard the occurrence of callipodidans in China and SE Asia as secondary, resulting from dispersal from Laurasia. This explanation would imply a cladistically subordinate position of the Chinese and SE Asian callipodidans (see, e.g. Enghoff 1993) which, in the case of Sinocallipodidae, is in conflict with the assumed basal position of this family. A phylogenetic analysis is obviously needed in order to better understand the evolution and biogeography of the order Callipodida.

Identification key to the species of *Sinocallipus*

1(4) body and antennae uniformly yellow-whitish; eye unpigmented, with less than 20 ocelli **2**

2(3) 55–56 PT; 16 ocelli; crests low, flattened; cannula of gonopods short and coiled; Xiao cave, China .... ***S. simplipodicus***

3(2) 59–61 PT, 10–11 ocelli; crests well-developed, ribbed; cannula long and straight; caves in Khammouan Province, Laos .... ***S. jaegeri* sp. n.**

4(1) either body or antennae with brown pigment; eye black, with more than 30 ocelli **5**

5(6) body brown with light middorsal band stretching from PT 5 to the body end; first four PT, anterior part of head and antennal articles 6 and 7 snow white; eye with 45–50 ocelli; antennae short, slightly extending beyond posterior edge of PT 4, femoroid with two slender acicular and one shorter and subfalcate terminal projections; surroundings of Sri Wilai Temple, Thailand .... ***S. thai***

6(5) body generally white-yellowish, sometimes mottled gray-brownish; antennae long, extending beyond the posterior edge of PT 7 when folded backwards; eye with less than 40 ocelli; femoroid with three slender acicular and one shorter and subfalcate terminal projections **7**

7(8) length of antennae *ca* 5.5 mm; 3+3 crests between ozopores on midbody PT, gonocoxal process *k* 2/3 length of process *g*; cave in Luan Prabang Province, Laos .... ***S. steineri* sp. n.**

8(7) length of antennae more than 7 mm; 5+5 crests between ozopores on midbody PT; gonocoxal process *k* half length of process *g* or smaller; caves in Vietnam **9**

9(10) body length *ca* 70 mm; gonocoxal process *g* long, more than 3 times the length of process *k*; paraprocts divided into two almost equal in size sclerites; caves in Quang Binh Province, Vietnam .... ***S. deharvengi* sp. n.**

10(9) body length *ca* 50 mm; gonocoxal process *g* long, *ca* 1.5 times the length of process *k*; paraprocts divided into larger ventral and smaller dorsal sclerites; caves on Cat Ba Island, Vietnam .... ***S. catba* sp. n.**

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RESEARCH ARTICLE

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New earthworm species of the genus *Amynthas* Kinberg, 1867 from Thailand (Clitellata, Oligochaeta, Megascolecidae)

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Abstract

Four new species of terrestrial earthworms from the *zebrus*-group in the genus *Amynthas* Kinberg, 1867, are described from Nan province, north Thailand: *A. phatubensis* **sp. n.**, from Tham Pha Tub Arboretum, *A. tontong* **sp. n.**, from Tontong Waterfall, *A. borealis* **sp. n.**, from Chaloemprakiat district, and *A. srinan* **sp. n.**, from Srinan National Park. After comparing with the two closely related Laos species *A. chandyi* Hong, 2008 and *A. namphouinensis* Hong, 2008, the four new species show clear morphological differences, and also it is confirmed that there are no previous records of the species described here. *Amynthas phatubensis* **sp. n.** is the largest (longest) sized of these earthworms and is the only species that lives in limestone habitats. The genital characters are different among them and also from the two Laotian species. Molecular systematics would be a good method for further analysis of the diversity and species boundaries in SE Asian *Amynthas*.

Keywords
Amynthas, Earthworm, Taxonomy, New species, Thailand

Introduction

Previous taxonomic publications on, or including, the Megascolecidae (*sensu* Blakemore 2000) of Thailand are comprised of those of Gates (1972), Sims and Easton (1972) and Blakemore (2006b, 2008, 2011) and Blakemore et al. (2007). Collectively, in these publications, 32 species are recorded for Thailand, belonging to five genera (*Amynthas* Kinberg, 1867, *Lampito* Kinberg, 1867, *Metaphire* Sims & Easton, 1972, *Polypheretima* Michaelsen, 1934 and *Perionyx* Perrier, 1872). The genus *Amynthas* is one of the dominant terrestrial earthworm genera that occurs throughout Thailand and nearby countries. From the classifications by Sims and Easton (1972) and reports by Blakemore (2006b, 2011) and Somniyam (2008), it would seem that 14 species from this genus have been recorded from many areas in Thailand (Table 1). However, in addition Kosavititkul (2005) has reported six species of *Amynthas* from Khao Yai National Park, which included three unknown species, Chantaravisoot (2007) reported five species of *Amynthas* from various areas in Thailand that were all commented to be new to science, and Somniyam (2008) recorded seven *Amynthas* species from Nakhonratchasima province of which many are still unidentified. Outside of Thailand, recent publications have included that by James (2004) who described a new species (*A. heaneyi*) from the Philippines; Shen and Yeo (2005) who reported four *Amynthas* species in Singapore, and Hong (2008) who described two species (*A. chandyi* and *A. namphouinensis*) from Laos, and also reported some publications by Vietnamese who studied the earthworm fauna in Laos and described *A. xuongmontis*. From the above data it is clear that there are still many species waiting to be discovered and described. The Animal Systematics Research Unit, Chulalongkorn University's members have surveyed terrestrial earthworms throughout Thailand since 2005 and a part of their results has been summarized in Chantaravisoot (2007). In the present paper we describe an additional four new species belonging to the *zebrus*-group, a provisional assemblage designated by Sims and Easton (1972). Each of these new species is known only from its type locality, but as more intensive collecting is undertaken in Thailand and other Asian countries, the known range and habitats of these species may be extended. The habitats of all four new species were in the topsoil layer covered with leaf litter of deciduous forests. The localities were in Nan province, in the north of Thailand, as shown in Figure 1.

Since none of the four species described in this paper seems to fit the descriptions of species described in the past, the purpose of this paper is to formally describe these species as new to science. Their descriptions follow.

Table 1. Morphological characteristics comparison of *Amynthas* species recorded in Thailand. The morphological characters are from the original description of each nominal species, except for the character with (*) are from Gates (1972). (**) indicate the known localities of *Amynthas* species in Thailand taken from Gates (1972), Kosavititkul (2005) and Somniyam (2008). Species group are as per Sims and Easton (1972)

Species	Species group	Body length (mm)	Number of segments	Spermathecal pores	Genital markings	Genital marking glands	Seminal vesicles	Prostate glands	Intestinal caeca	Distribution**
A. hupbonensis (Stephenson, 1931)	aeruginosus	225	142	7/8–8/9	absent	absent	large in XI, XII	XVI–XX	manicate, XXVII–	Chonburi
A. alexandri (Beddard, 1900)	corticis	145	133	5/6–8/9	absent	absent	XI, XII	XVII–XX	simple, XXVII–XX	Chiengrai, Chiengmai, Nakornratchasima, Bangkok, Chonburi
A. comptus (Gates, 1932)	corticis	197–260*	120–134*	5/6–8/9	three trios on 18/19–20/21	sessile	larger in XI, XII	XVIII	simple, XXVII–XXIII	Phrae
A. exiguus austrinus (Gates, 1932)	corticis	33–68	73–102	5/6–8/9	two pairs on 17/18,18/19	absent	small in XI, XII	XVII–XX	simple, XXVII–XXIV	Chiengmai
A. exiguus exiguus (Gates, 1930)	corticis	43	90	5/6–8/9	paired on vii, viii, xix, xx	absent	small in XI, XII	XVII–XIX	simple, XXVII–XXIV	Phrae
A. longicauliculatus (Gates, 1931)	corticis	170	138	5/6–8/9	three pairs on 18/19–20/21	sessile	XI, XII	XVIII	simple, xxvii-xxiv	Chiengmai, Lumphun, Nakornratchasima
A. manicata decorosa (Gates, 1932)	corticis	40	60	5/6–8/9	one pair on xviii	sessile	large in XI, XII	XVII–XIX	manicate, XXVII–XXII	Chiengmai
A. mekongianus (Cognetti, 1922)	corticis	1 meter	370	5/6-8/9	absent	absent	10/11-11/12	XVII-XVIII	simple, XXVII-XXIII	Chiengrai

Species	Species group	Body length (mm)	Number of segments	Sperma-thecal pores	Genital markings	Genital marking glands	Seminal vesicles	Prostate glands	Intestinal caeca	Distribution**
A. defecta (Gates, 1930)	gracilis	>78	>49	5/6–7/8	absent	absent	small in XI, XII	absent	manicate, XXVII–XXVI	Nakornratchasima
A. gracilis (Rosa, 1891)	gracilis	100	88–95	5/6–7/8	clusters on xviii	stalked*	XI, XII*	XVII–XXIII	simple, XXVII–XXIV*	Dor Kiu Koh Ma, north Thailand
A. papulosus (Rosa, 1896)	gracilis	45–50	110–115	5/6–7/8	transverse row on XVII–XIX	stalked*	XI, XII	XVI–XXI	simple, XXVII–XXII*	Yala
A. morrisi (Beddard, 1892)	morrisi	52	93	5/6–6/7	near spermathecal pore	stalked	XI, XII*	XVII–XXIII*	simple, XXVII–XXIV*	Chiengmai
A. fucosus (Gates, 1933)	sieboldi	120	114	6/7–8/9	two pairs on 17/18, 18/19	sessile	large in XI, XII	XVII–XX	simple, XXVII–XVII	Nakornratchasima
Amynthas siam. Blakemore, 2011	sieboldi	>70	>73	6/7-8/9	one pair postsetal on XVIII	sessile	XI, XII	XVIII-	simple, XXVII-	Sakon Nakhon

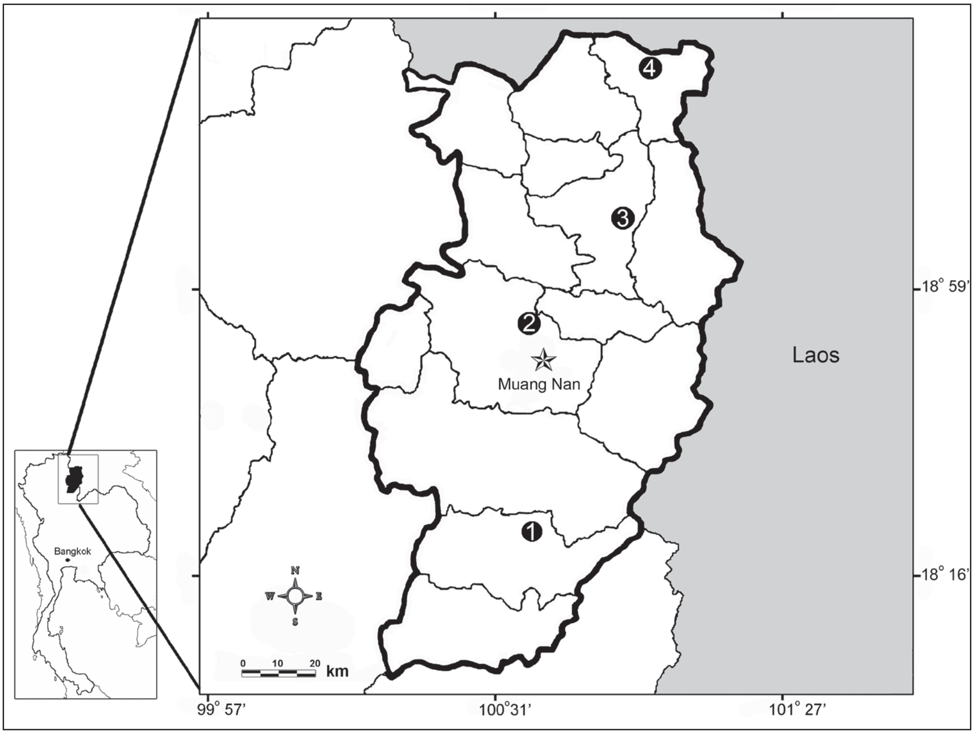

Figure 1. Map of type locality of **1** *Amynthas srinan* sp. n. from Srinan National Park, Nan province, **2** *Amynthas phatubensis* sp. n. from Tham Pha Tub Arboretum, Nan province, **3** *Amynthas tontong* sp. n. from Tontong Waterfall, Pua district, Nan province and **4** *Amynthas borealis* sp. n. from a small hill near Chaloemprakiat district, Nan province.

Material and methods

Earthworms were collected from deciduous forests in many areas in Nan province, north of Thailand, by carefully digging up the topsoil near casts and by hand sorting the leaf litter. The worms were killed in 30% (v/v) ethanol, photographed, transferred to 5% (w/v) formalin for fixation for approximately 12 hours, and then transferred to 70% (v/v) ethanol for longer term preservation and subsequent morphological studies.

Duplicate specimens and/or tissue samples (in the cases of morphotypes determined to be unique on field inspection) were preserved in 95% ethanol for molecular data and DNA barcoding. Tissues were sent to the Canadian Center for DNA Barcoding (Hebert et al. 2003a, b) and processed according to their standard protocols (Hajibabaei et al. 2005; Ivanova et al. 2006; Ratnasingham and Hebert 2007). DNA barcode data are provided for paratype specimens of the first two species described in this paper. The sequences were aligned with Clustal X using default settings, and the resulting Neighbor-Joining tree (Saitou and Nei 1987) was used to identify barcode clusters. These clusters were matched to OTUs identified from quick examination of external characters. Inter- and intra- cluster genetic distances were calculated in MEGA

4 (Tamura et al. 2007) using the Kimura two parameter distance (Kimura 1980) using gamma-distributed rates among sites, pairwise deletion of sites with missing data, and using all substitution types and codon positions.

The descriptions of each species were made during observation under a Stemi DV 4 ZEISS stereoscopic light microscope. Drawings were made of the body segments and the distinct external characters and internal organs, as mentioned above, and are shown in Figures 2–5 for the four new species, respectively. The number of segments and the body width and length were measured in both full adults and juveniles, and are presented as the range (min-max) and mean±one standard deviation.

Type specimens housed at the Department of Biology, Faculty of Science, National University of Laos, Vientiane, Laos (BDNUL), of the two closely related Laos species, *A. chandyi* Hong, 2008 and *A. namphouinensis* Hong, 2008, have been critically studied and compared with the new species of this report.

Holotype and paratype specimens have been deposited in the Chulalongkorn University, Museum of Zoology, Bangkok, Thailand (CUMZ). Additional paratypes are housed in the Biozentrum Grindel und Zoologisches Museum, Hamburg, Germany (UHH), and the Natural History Museum, London (NHM).

Anatomical abbreviations: fp, female pore; ic, intestinal caeca; mp, male pores; pg, prostate gland; sc, spermathecae; sp, spermathecal pores; sv, seminal vesicles.

Systematics

Genus *Amynthas* Kinberg, 1867

Type species. *Amynthas aeruginosus* Kinberg, 1867, by monotypy.

Amynthas phatubensis Panha & Bantaowong, sp. n.

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http://species-id.net/wiki/Amynthas_phatubensis
Figs 1, 2

Description of holotype: Dimensions; 110 mm by 4.3 mm at segment X, 4.3 at segment XX, 4.0 mm at clitellum; body cylindrical with 108 segments. Setae regularly distributed around segmental equators, numbering 51 at VII, 60 at XX, 15 between mp, setae formula AA:AB:ZZ:ZY= 1:1:1:1 at XIII with no ventral gaps. Single fp at XIV. Prostomium epilobic with tongue open. First dorsal pore at 5/6. Clitellum annular XIV–XVI with no setae.

A pair of mp is located ventro-laterally in XVIII, or at 9th seta line, 0.33 circumference apart ventrally, convex structure; distance between mp 4.2 mm. Porophores (protuberances bearing male aperture), papilla-like structures. Each mp surrounded by six flat, circular

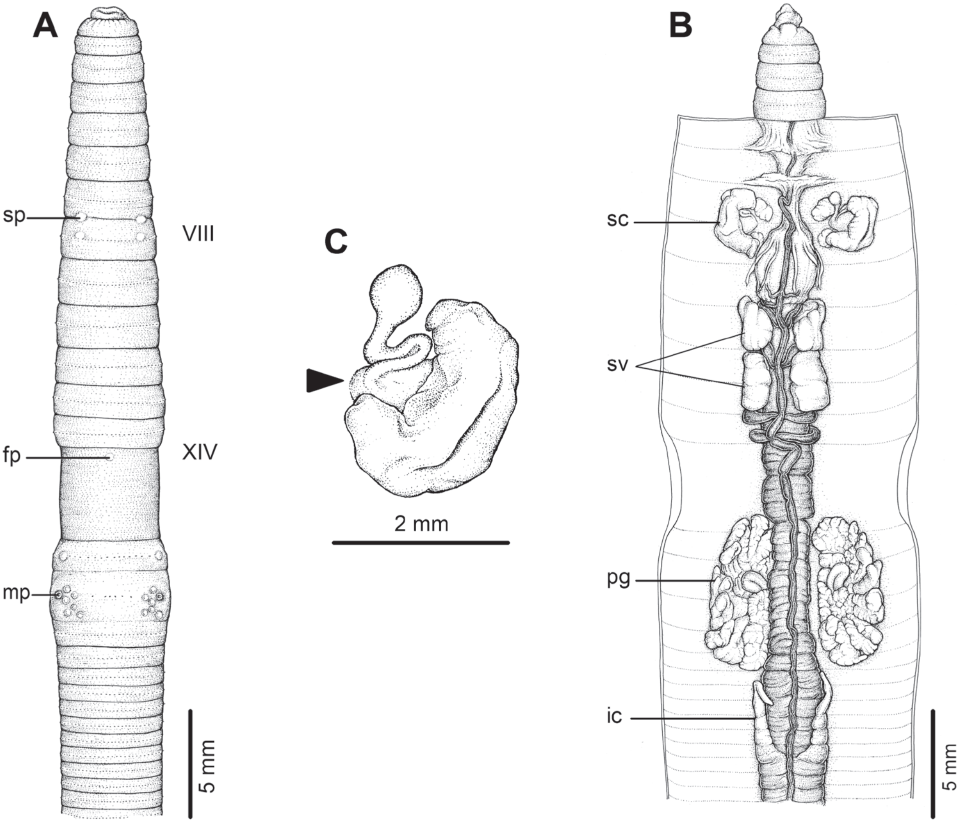

Figure 2. External and internal morphology of holotype (CUMZ 3204) of *Amynthas phatubensis* sp. n. **A** External ventral view, **B** internal dorsal view and **C** spermatheca, and black arrow indicates the connection of the spermatheca and spermathecal pore.

genital markings almost the same diameter as mp, also one pair is equatorial in XVII in line with the male pores. One pair of sp in intersegmental furrow 7/8, distance between pores 0.32 circumference ventrally apart; distance between sp 3.5 mm. Genital markings, rounded, flat, located close to sp, postsetal paired on VII very near 7/8, presetal paired on VIII.

Septa 5/6 and 6/7 thick, 7/8 thin, 8/9 and 9/10 absent, 10/11–13/14 thin. Gizzard large within VIII–X, intestinal origin in XV, no lymph glands observed. Typhlosole small from XXVII. Intestinal caeca originate from XXVII extending forward to XXIII, simple, long finger-shape. Hearts esophageal in X–XIII. Holandric; testes and funnels in ventrally joined sacs in X–XI. Seminal vesicles paired in XI–XII. Prostates in XVII–XX; prostatic ducts U-shape. Genital marking glands absent.

Ovaries in XIII. Sc one pair in VIII; ampulla large ovate sac, duct stout, short; long stalked diverticulum, convoluted kinks enclosed within membrane, spherical knob terminal. No nephridia on spermathecal ducts. A large sessile genital marking gland corresponding to each external genital marking in VII–VIII.

All the key morphological characters of the holotype and paratype specimens are given in Table 2.

Variation: The holotype measures 110 mm body length with 108 segments; the twenty one paratypes range in size from 80–148 mm (108±21.93 mm) body length with 85–114 segments (Table 2).

Type locality: Tham Pha Tub Arboretum, Nan province, Thailand, 18°51'16.4"N, 100°44'10.1"E, 265 meters elevation (11th October 2009). We also collected another lot of further specimens from Tontong Waterfall, Nan province (location 3 in Figure 1), which is located about a hundred kilometers north of the type locality.

Etymology: This species was named after the type locality, Tham Pha Tub Arboretum.

Type material: The holotype (CUMZ 3204) and 15 paratypes (CUMZ 3205) and 10 paratypes (CUMZ 3212) are deposited in Chulalongkorn University, Museum of Zoology. Another four paratypes will be deposited in the Biozentrum Grindel und Zoologisches Museum, Hamburg, Germany (UHH), and three paratypes in the Natural History Museum, London (NHM).

Habitat: Found in the top soil at about 10 cm depth, the soil surface was covered with leaf litter in a deciduous limestone forest at Tham Pha Tub Arboretum. The soil was carefully dug close to the casts. Many ariophantid snails, *Cryptozona siamensis* Pfeiffer, 1856 were on the ground or under leaf litter.

Diagnosis: *Amynthas phatubensis* sp. n. is a medium to large sized terrestrial earthworm with a pair of mp surrounded by six genital papillae on segment XVIII. Within the *zebrus*-group, this species is diagnosed by the unique combination of dorsal pores in 5/6, simple digitate caeca, ventrally joined testis sacs, genital marking glands in the spermathecal segments, and the spermathecal characters of the large ovate ampulla, stalked diverticulum whose folds are membrane-bound, and spherical knob terminal diverticulum sac.

Remarks: *Amynthas phatubensis* sp. n. has very simple characteristics of the genus, but among these, only the superficial male pores are external. In most newly collected specimens it was difficult to observe the pores or marks on the bodies. However, after preservation they can be seen more clearly. The internal organs are much more easily discerned. This new species is quite distinct when compared to the two closely related species from Laos, *A. chandyi* Hong, 2008 and *A. namphouinensis* Hong, 2008, which belong in the same *zebrus*-group. The two Laos species are a little bit smaller than *A. phatubensis* sp. n., especially *A. chandyi*. Even though *A. namphouinensis* is much closer in appearance to *A. phatubensis* sp. n., there are distinct differences between the type specimens (Figs 6 and 7). For example, the distance between the mp of *A. phatubensis* sp. n. is 4.2 mm for the holotype and range from 3.0–4.5 mm (4.27±0.57mm), while for *A. namphouinensis* this was significantly smaller, ranging from 1.4–1.5 mm. The distance between a pair of sp is also different, being 3.5–4.5 mm (4.12±0.4 mm) for *A. phatubensis* sp. n. and 1.4–2.0 mm in *A. namphouinensis*. The distance between the male pores as a fraction of the estimated circumference of the 18th segment is 0.30–0.33 in *A. phatubensis* sp. n., but 0.10–0.14 circumference apart in *A. namphouinensis*.

Table 2. Holotype and Paratype dimension and other morphological characteristics of *Amynthas phatubensis* Panha & Bantaowong, sp. n.

Characters / Types	Body length (mm)	Number of segments	Location of genital markings		First dorsal pore	Number of setae			Prostate glands	Intestinal caeca
			Preclitellum	Postclitellum		VII	XX	Between male pore		
Holotype CUMZ 3204	110	108	VII, VIII	XVII, XVIII	5/6	51	60	15	XVII–XX	XXVII–XXIII
Paratype CUMZ 3205										
1	90	96	VII, VIII	XVIII	5/6	60	58	15	XVII–XXI	XXVII–XXIV
2	105	107	VII, VIII, IX	XVII, XVIII, XIX	5/6	52	58	12	XVII–XX	XXVII–XXIV
3	100	105	VII, VIII, IX	XVIII	5/6	53	60	9	XVII–XX	XXVII–XXIV
4	80	86	VII, VIII	XVII, XVIII, XIX	5/6	53	65	13	XVII–XX	XXVII–XXIV
5	120	96	VII, VIII	XVIII	5/6	58	68	11	XVII–XX	XXVII–XXIV
6	101	85	VII, VIII	XVIII	5/6	51	59	9	XVII–XX	XXVII–XXIV
7	131	86	VII, VIII	XVII, XVIII	5/6	64	67	15	XVII–XXI	XXVII–XXII
8	108	98	VII, VIII	XVII, XVIII	5/6	58	62	15	XVII–XXI	XXVII–XXII
9	116	99	VII, VIII	XVII, XVIII	5/6	53	64	11	XVII–XXI	XXVII–XXIII
10	89	92	VII, VIII	XVII, XVIII	5/6	64	58	12	XVII–XX	XXVII–XXIV
11	99	106	VII, VIII, IX	XVII, XVIII	5/6	60	63	13	XVII–XXI	XXVII–XXIV
12	112	112	VII, VIII	XVII, XVIII	5/6	52	58	11	XVII–XX	XXVII–XXIII
13	142	110	VII, VIII	XVII, XVIII	5/6	49	58	7	XVII–XX	XXVII–XXIV
14	137	108	VII, VIII, IX	XVII, XVIII	5/6	62	65	11	XVII–XX	XXVII–XXIII
15	80	85	VII, VIII, IX	XVII, XVIII	5/6	54	60	13	XVII–XX	XXVII–XXIV
16	89	111	VII, VIII, IX	XVII, XVIII	5/6	57	59	14	XVII–XXI	XXVII–XXIII
17	84	105	VII, VIII	XVII, XVIII	5/6	52	59	11	XVII–XX	XXVII–XXIV
18	148	112	VII, VIII	XVII, XVIII	5/6	51	58	12	XVII–XX	XXVII–XXII
19	109	114	VII, VIII	XVII, XVIII	5/6	64	59	12	XVII–XX	XXVII–XXII
20	144	107	VII, VIII	XVII, XVIII	5/6	53	60	11	XVII–XXI	XXVII–XXIV
21	84	108	VII, VIII	XVII, XVIII	5/6	64	61	15	XVII–XX	XXVII–XXII

Moreover, *A. phatubensis* sp. n. has no genital marking glands on segments XVII–XIX, where *A. namphouinensis* has sessile genital marking glands, but contains two distinct genital marking glands located close to sc that are absent in *A. namphouinensis.*

Two populations of *A. phatubensis* sp. n. were sampled, one from the type locality and one from Tontong waterfall. Distinct DNA barcode clusters corresponding to these populations had intra-cluster Kimura 2 parameter distances of 0.023 (N=9) and 0.016 (N=5) respectively. The inter-cluster divergence between the two populations is 0.084. Based on the morphological unity and the fact that the divergence is less than that usually seen between congeneric species pairs of earthworms (Chang et al. 2007; Pérez-Losada et al. 2005, James et al. 2010), we choose to maintain the two populations as representing one species. By contrast, the inter-cluster divergence between these populations and three other morpho-species with the same spermathecal battery, from the same two sites is in the range of 0.269-0.294. A consensus sequence from the type locality specimens is in Appendix 1. Another use of COI barcode sequence from type material is in Blakemore et al. (2010).

Amynthas tontong **Panha & Bantaowong, sp. n.**

urn:lsid:zoobank.org:act:3317146B-143D-4EFC-A0C9-60262073BAFF
http://species-id.net/wiki/Amynthas_tontong
Figs 1, 3

Description of Holotype: Dimensions; 53 mm by 2.7 mm at segment X, 2.6 at segment XX, 2.2 mm at clitellum; body cylindrical with 80 segments. Setae regularly distributed around segmental equators, numbering 42 at VII, 52 at XX, no visible setae between mp, setae formula AA:AB:ZZ:ZY= 1.5:1:1:1 at XIII. Single fp at XIV. Prostomium epilobic. First dorsal pore at 5/6. Clitellum annular XIV–XVI with no setae.

A pair of indistinct rounded mp in XVIII, 0.19 mm circumference apart ventrally; distance between mp 1.0 mm at 5th seta line. Genital markings closely paired located medial to male pore level in intersegment 18/19. Sp paired in 7/8 at 4th seta line, each small, lip-like structure within porophore, 0.10 circumference apart ventrally; distance between sp 1.0 mm. Genital markings near sp absent.

Septa 5/6 and 6/7 thick, 7/8 thin, 8/9 and 9/10 absent 10/11–13/14 thin. Gizzard large within VIII–X, intestinal origin in XV, no lymph glands observed. Typhlosole small from XXVII. Ic originated from XXVII extending forward to XXV, simple finger-shape. Hearts esophageal in X–XIII. Holandric; testes and funnels in ventrally joined sacs in X–XI. Sv paired in XI–XII. Prostates in XVIII; prostatic ducts long slender with U-shape. Genital marking glands absent.

Ovaries in XIII. Sc one pair in VIII; ampulla thumb shape, duct stout, shorter than ampulla. Diverticulum slender stalk with spherical knob terminal, no genital marking glands observed.

All the key morphological characters of the holotype and paratype specimens are given in Table 3.

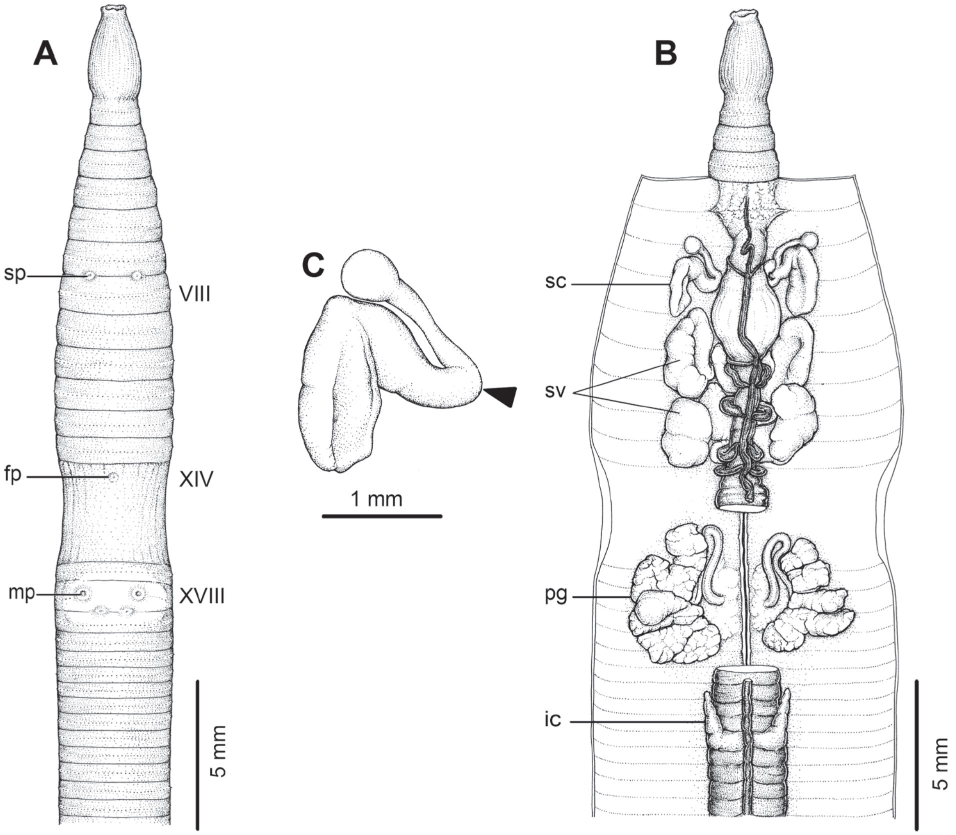

Figure 3. External and internal morphology of holotype (CUMZ 3206) of *Amynthas tontong* sp. n. **A** External ventral view, **B** internal dorsal view and **C** spermatheca, and black arrow indicates the connection of the spermatheca and spermathecal pore.

Variation: The holotype measures 53 mm body length with 80 segments; the three paratypes range in size from 39–41 mm (40.33±1.15 mm) body length with 71–74 segments (Table 3).

Type locality: Tontong Waterfall, Nan province, Thailand, 19°12'35.9"N, 101°04'13.7"E, 1,128 meters elevation (10th October 2009).

Etymology: This species was named after the type locality, Tontong Waterfall.

Type material: The holotype (CUMZ 3206) and two paratypes (CUMZ 3207) are deposited in Chulalongkorn University, Museum of Zoology. Another paratype will be deposited in the Biozentrum Grindel und Zoologisches Museum, Hamburg, Germany (UHH).

Habitat: Found in the top soil at about 10 cm depth, the soil surface covered with leaf litter of deciduous forest which originated at the Tontong Waterfall area. The soil was carefully dug close to surface casts. Most surrounding areas have been modified to agricultural fields.

Table 3. Holotype and Paratype dimension and other morphological characteristics of *Amynthas tontong* Panha & Bantaowong sp. n.

Characters / Types	Body length (mm)	Number of segments	Genital markings	First dorsal pore	Number of setae		Between male pore	Prostate glands	Intestinal caeca
					VII	XX			
Holotype CUMZ 3206	53	80	XVIII	5/6	42	52	0	XVII–XX	XXVII–XXIV
Paratype CUMZ 3207									
1	41	71	XVIII	5/6	41	53	0	XVI–XVIII	XXVII–XXV
2	39	74	XVIII	5/6	42	52	0	XVII–XX	XXVII–XXIV
3	41	73	XVIII	5/6	46	55	0	XVII–XIX	XXVII–XXIII

Diagnosis: *Amynthas tontong* sp. n. is a small sized terrestrial earthworm with a close indistinct pair of male pores with a pair of genital markings in intersegment 18/19. Spermathecae consists of a thumb shaped ampulla and a spherical terminal knob shaped diverticulum. Genital marking glands absent, first dorsal pore in 5/6, intestinal caeca simple, intestinal origin XV, septa 8/9/10 absent, testis sacs joined ventrally.

Remarks: *Amynthas tontong* sp. n., along with *A. srinan* sp. n. and *A. exiguus exiguus*, is one of the smallest sized *Amynthas* ever recorded in Thailand. The basic external characters are easily seen in both newly collected and preserved materials. Compared with the two other closely related species from Laos, *A. chandyi* Hong, 2008 and *A. namphouinensis* Hong, 2008, which belong in the same *zebrus*-group, *A. chandyi* is similar to *A. tontong* sp. n. However, it differs in the specific details of the significant characters, such as the distance between the mp in *A. tontong* sp. n. is 1.0 mm for the holotype and ranged from 1.0–1.2 mm (0.93±0.12 mm), while in *A. chandyi* it ranged from 1.5–2.4 mm. The distance between the male pores as a fraction of the estimated circumference of the 18th segment is 0.15–0.19 in *A. tontong* sp. n., but 0.14–0.32 in *A. chandyi*. The arrangement of the genital markings of both species are totally different, and the distance between a pair of sp is also different, being 0.8–1.0 mm (1.1±0.1 mm) in *A. tontong* sp. n. and 1.2–1.5 mm for *A. chandyi*. Moreover, *A. tontong* sp. n. has no genital markings near to the sp, whilst *A. chandyi* exhibits circular genital markings in various locations, paired or single mid ventral in VII, VIII; usually 3 or 4 in total.

Alcohol-preserved paratype specimens of *A. tontong* sp. n. belonged to a single DNA barcode cluster, with an intra-cluster divergence of 0.005 (N=3), and diverging from *A. phatubensis* sp. n. by 0.294, and by 0.189 for an undescribed species. An undescribed morph at Tham Pha Tub diverged by 0.100, and may represent a subspecies. A consensus sequence is in Appendix 1.

Amynthas borealis Panha & Bantaowong, sp. n.

urn:lsid:zoobank.org:act:C2BE17F8-A721-4736-9809-EF9ABDAB0C03
http://species-id.net/wiki/Amynthas_borealis
Figs 1, 4

Description of Holotype: Dimensions; 54 mm by 3.5 mm at segment X, 3.8 at segment XX, 3.5 mm at clitellum; body cylindrical with 89 segments. Setae regularly distributed around segmental equators, numbering 39 at VII, 51 at XX, no visible setae between mp, setae formula AA:AB:ZZ:ZY= 2:1:1.5:1 at XIII. Single fp at XIV. Prostomium epilobic. First dorsal pore at 5/6. Clitellum annular XIV–XVI with no setae.

Mp pocket-like structures indistinctly occur in XVIII, 0.10 circumference apart ventrally; distance between mp 1.0 mm; porophores small, lip-like and surrounded by an elevated skin fold at medial pores, and there is a long ridge with a sharp posterior boundary traversing the body in front of the mp. Genital markings absent. Sp paired in 7/8 at 4th seta line, 0.10 circumference apart ventral; distance between sp 1.0 mm. Genital markings absent.

Septa 5/6 and 6/7 thick, 7/8 thin, 8/9 and 9/10 absent, 10/11–13/14 thin. Gizzard large within VIII–X, intestinal origin in XV, no lymph glands observed. Typhlosole small from XXVII. Ic originated from XXVII extending forward to XXV, simple finger-shape. Hearts esophageal in X–XIII. Holandric; testes and funnels in ventrally joined sacs in X–XI. Sv paired in XI–XII. Prostates in XVIII; prostatic ducts long slender bent in U-shape. Genital marking glands absent.

Ovaries at XIII. Sc one pair in VIII; ampulla large sac-shape, flattened by gizzard, narrow duct shorter than ampulla. Diverticulum with elongated tubular shape, stalk attached to duct near body wall, with no genital marking glands.

All the key morphological characters of the holotype and paratype specimens are given in Table 4.

Variation: The holotype measures 54 mm body length with 89 segments; the eight paratypes range in size from 42–45 mm (42.87±1.25 mm) body length with 77–87 segments (Table 4).

Type locality: Chaloemprakiat district, Nan province, Thailand, 19°34'48.5"N, 101°04'53.1"E, 513 meters elevation (7th August 2010).

Etymology: The specific epithet "*borealis*" derived from Latin word "boreal" mean "north". This name refers to the location of type locality in the north of Thailand.

Type material: The holotype (CUMZ 3208) and seven paratypes (CUMZ 3209) are deposited in Chulalongkorn University, Museum of Zoology. Another two paratypes will be deposited in the Biozentrum Grindel und Zoologisches Museum, Hamburg, Germany (UHH), and another two paratypes in the Natural History Museum, London (NHM).

Habitat: Found in the top soil at about 10 cm depth, the soil surface covered with the leaf litter of a deciduous limestone forest, mostly disturbed. The soil was carefully dug close to the casts.

Diagnosis: *Amynthas borealis* sp. n. is a small sized terrestrial earthworm small male pores, a transverse ridge anterior to the male pores in XVII, and no genital mark-

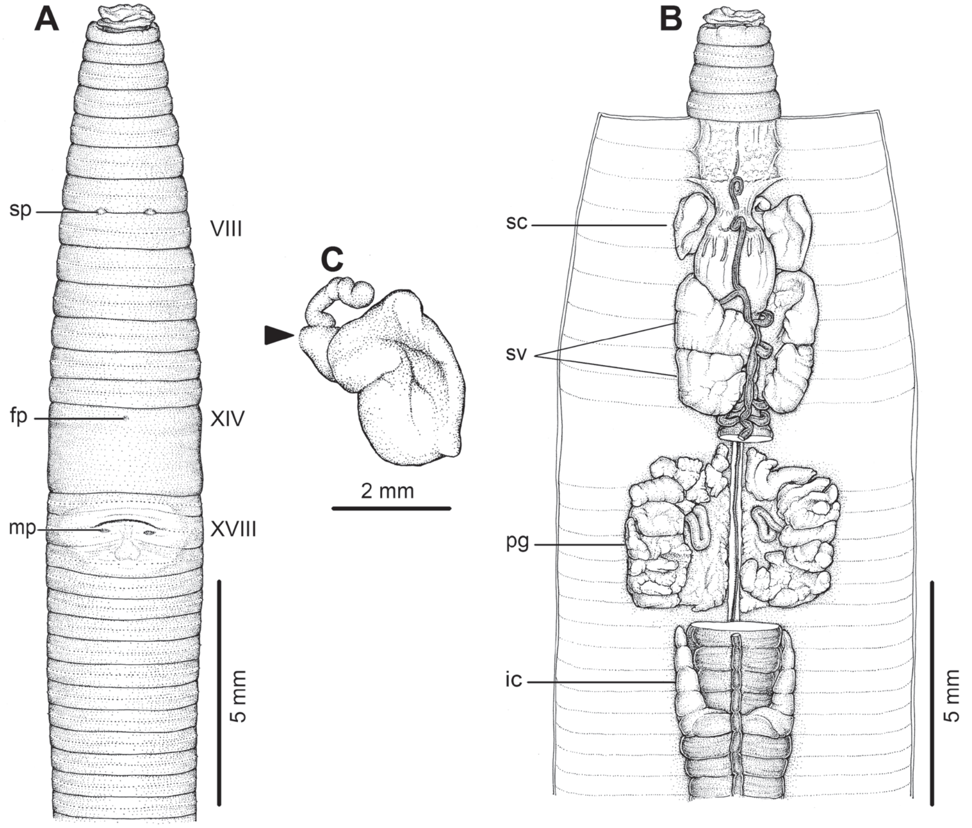

Figure 4. External and internal morphology of holotype (CUMZ 3208) of *Amynthas borealis* sp. n. **A** External ventral view, **B** internal dorsal view and **C** spermatheca, and black arrow indicates the connection of the spermatheca and spermathecal pore.

ings. One pair of sc in VIII, each spermathecae consists of a large sac-shaped ampulla and elongated tubular shaped diverticulum. Testis sacs joined ventrally, intestinal origin XV, intestinal caeca simple, first dorsal pore in 5/6.

Remarks: *Amynthas borealis* sp. n. is one of the smaller *Amynthas*. The characteristic male field is difficult to see in newly collected specimens but can be clearly observed after preservation. Compared with the two other closely related species from Laos, *A. chandyi* and *A. namphouinensis*, which belong in the same *zebrus*-group, *A. chandyi* is similar to *A. borealis* sp. n. However, distinctive differences include the distance between mp of the new species, being 1.0 mm in the holotype with a range of 0.8–1.0 mm (0.95±0.09 mm) in *A. borealis* sp. n. compared to 1.5–2.4 mm. The distance between the male pores as a fraction of the estimated circumference of the 18th segment is 0.10–0.14 in *A. borealis* sp. n., but 0.14–0.32 in *A. chandyi*. There are no genital markings in the new species; the distance between a pair of sp is also different, being 0.5–1.0 mm (0.9±0.19 mm) in the new species compared to 1.2–1.5 mm for *A. chan-*

Table 4. Holotype and Paratype dimension and other morphological characteristics of *Amynthas borealis* Panha & Bantaowong, sp. n.

Characters / Types	Body length (mm)	Number of segments	Genital markings	First dorsal pore	Number of setae		Between male pore	Prostate glands	Intestinal caeca
					VII	XX			
Holotype CUMZ 3208	54	89	Absent	5/6	39	51	0	XVII–XIX	XXVII–XXV
Paratype CUMZ 3209									
1	45	87	Absent	5/6	51	48	0	XVII–XX	XXVII–XXIV
2	42	78	Absent	5/6	49	45	0	XVIII–XIX	XXVII–XXIII
3	44	79	Absent	5/6	51	50	0	XVII–XX	XXVII–XXIII
4	42	86	Absent	5/6	54	41	0	XVIII–XIX	XXVII–XXIV
5	44	85	Absent	5/6	40	40	0	XVIII–XIX	XXVII–XXIV
6	42	85	Absent	5/6	46	48	0	XVII–XIX	XXVII–XXIV
7	42	77	Absent	5/6	44	50	0	XVII–XX	XXVII–XXV
8	42	83	Absent	5/6	48	52	0	XVII–XIX	XXVII–XXV

dyi. Moreover, *A. borealis* sp. n. has no genital marking glands at all, whilst *A. chandyi* exhibits circular genital markings in various locations, paired or single mid ventral in VII and VIII; usually 3 or 4 in total.

Amynthas srinan Panha & Bantaowong, sp. n.

urn:lsid:zoobank.org:act:C3EC91E6-B29A-4C72-908F-1858DE7F21DA
http://species-id.net/wiki/Amynthas_srinan
Figs 1, 5

Description of Holotype: Dimensions; 47 mm by 1.8 mm at segment X, 2.3 at segment XX, 2.3 mm at clitellum; body cylindrical with 77 segments. Setae regularly distributed around segmental equators, numbering 36 at VII, 42 at XX, four between mp, setae formula AA:AB:ZZ:ZY= 1.5:1:2:1 at XIII. Single fp at XIV. Prostomium epilobic with tongue open. First dorsal pore at 4/5 or 5/6. Clitellum annular XIV–XVI with no setae.

Mp on circular porophores in XVIII, 0.30 circumference apart ventrally; distance between mp 1.5 mm. Genital markings small, postsetal, closely paired near mid ventral

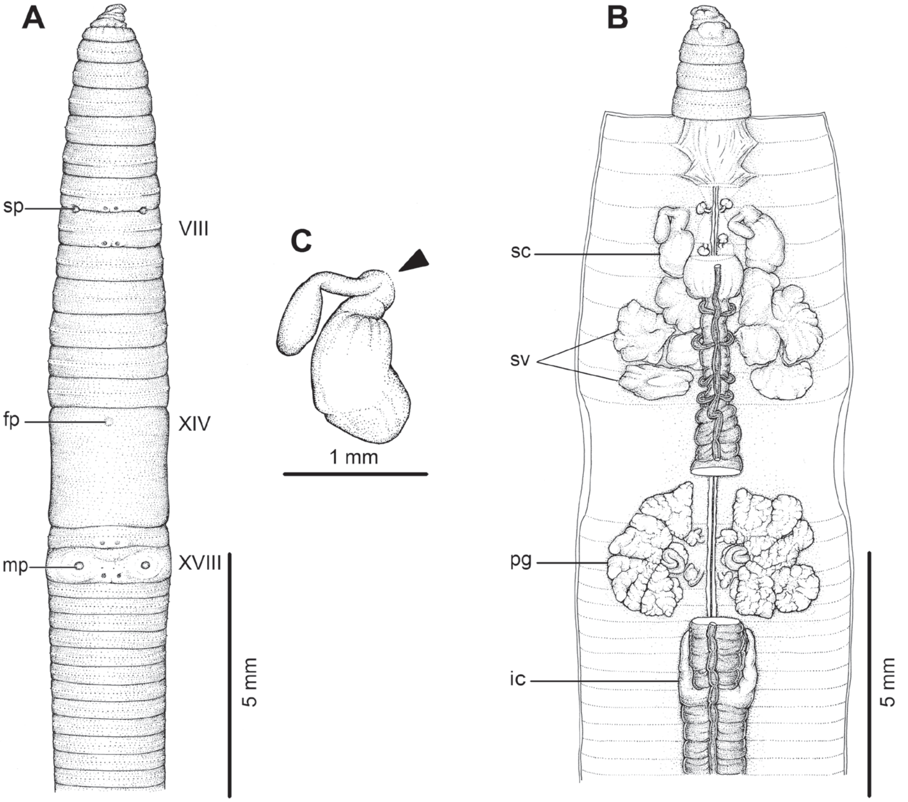

Figure 5. External and internal morphology of holotype (CUMZ 3210) of *Amynthas srinan* sp. n. **A** External ventral view, **B** internal dorsal view and **C** spermatheca, and black arrow indicates the connection of the spermatheca and spermathecal pore.

of XVII and XVIII. Sp paired in 7/8 at 6th setal lines, 0.26 circumference apart ventrally; distance between sp 1.5 mm. Genital markings tiny, closely paired on near mid ventral of VII and VIII.

Septa 5/6 and 6/7 thick, 7/8 thin, 8/9 and 9/10 absent, 10/11–13/14 thin. Gizzard globular within VIII–X, intestinal origin in XV, no lymph glands observed. Typhlosole small from XXVII. Ic originated from XXVII extending forward to XXIII, long finger-shape. Hearts esophageal in X–XIII. Holandric; testes and funnels in ventrally joined sacs in X–XI. Sv paired in XI–XII. Prostates in XVIII, extending between XVII–XX; prostatic ducts tightly folded twice. Genital marking glands paired in XVII and XVIII corresponding to external genital papillae, each consisting of a stalk with terminal multi-lobed glandular part.

Ovaries in XIII. Sc one pair in VIII; ampulla oval to kidney-shaped, with stout duct shorter than ampulla. Diverticulum with oval bulb terminal, stalk attached to duct near body wall. Genital markings stalked, corresponding to external genital papillae; each gland small consisting of a stalk with terminal multi-lobed glandular part.

Table 5. Holotype and Paratype dimension and other morphological characteristics of *Amynthas srinan* Panha & Bantaowong, sp. n.

Characters / Types	Body length (mm)	Number of segments	Location of genital markings		First dorsal pore	Number of setae		Between male pore	Prostate glands	Intestinal caeca
			preclitellum	postclitellum		VII	XX			
Holotype CUMZ 3210	47	77	VII, VIII	XVII, XVIII	5/6	36	42	4	XVII–XX	XXVII–XXIII
Paratype CUMZ 3211										
1	35	75	VII, VIII	XVII, XVIII	5/6	40	42	6	XVII–XX	XXVII–XXV
2	44	76	VII, VIII	XVII, XVIII	5/6	36	42	5	XVII–XX	XXVII–XXIV
3	39	65	VII, VIII	XVII, XVIII	5/6	37	46	4	XVIII–XX	XXVII–XXIV
4	44	70	VII, VIII	XVII, XVIII	5/6	36	49	5	XVII–XIX	XXVII–XXIV
5	47	78	VII, VIII	XVII, XVIII	5/6	38	45	4	XVII–XX	XXVII–XXIV
6	37	68	VII, VIII	XVII, XVIII	5/6	40	44	4	XVII–XX	XXVII–XXV
7	38	77	VII, VIII	XVII, XVIII	4/5	43	48	5	XVII–XXI	XXVII–XXIV
8	37	52	VII, VIII	XVII, XVIII	4/5	38	42	4	XVII–XXI	XXVII–XXV
9	35	57	VII, VIII	XVII, XVIII	4/5	41	44	4	XVII–XX	XXVII–XXIV
10	38	78	VII, VIII	XVII, XVIII	5/6	36	40	4	XVII–XX	XXVII–XXIV
11	42	77	VII, VIII	XVII, XVIII	4/5	42	47	4	XVII–XXI	XXVII–XXIII
12	45	77	VII, VIII	XVII, XVIII	5/6	39	45	5	XVII–XX	XXVII–XXIV
13	40	77	VII, VIII	XVII, XVIII	5/6	40	48	4	XVII–XIX	XXVII–XXV
14	39	77	VII, VIII	XVII, XVIII	5/6	39	47	4	XVII–XX	XXVII–XXIV
15	43	77	VII, VIII	XVII, XVIII	5/6	40	44	4	XVII–XX	XXVII–XXIII
16	40	75	VII, VIII	XVII, XVIII	5/6	41	49	4	XVII–XX	XXVII–XXIV
17	37	75	VII, VIII	XVII, XVIII	4/5	36	46	4	XVII–XIX	XXVII–XXIV
18	36	60	VII, VIII	XVII, XVIII	5/6	40	47	5	XVII–XX	XXVII–XXIV
19	39	75	VII, VIII	XVII, XVIII	5/6	37	44	4	XVII–XX	XXVII–XXIII

Characters / Types	Body length (mm)	Number of segments	Location of genital markings		First dorsal pore	Number of setae		Between male pore	Prostate glands	Intestinal caeca
			preclitellum	postclitellum		VII	XX			
20	47	78	VII, VIII	XVII, XVIII	4/5	36	42	4	XVII–XX	XXVII–XXV
21	42	71	VII, VIII	XVII, XVIII	5/6	40	46	4	XVII–XX	XXVII–XXIV
22	35	56	VII, VIII	XVII, XVIII	4/5	41	43	4	XVII–XIX	XXVII–XXIV
23	36	69	VII, VIII	XVII, XVIII	5/6	36	45	4	XVII–XX	XXVII–XXV
24	42	73	VII, VIII	XVII, XVIII	5/6	36	46	4	XVII–XX	XXVII–XXIV
25	44	76	VII, VIII	XVII, XVIII	4/5	39	47	6	XVI–XX	XXVII–XXV
26	35	69	VII, VIII	XVII, XVIII	5/6	36	44	4	XVII–XIX	XXVII–XXIII
27	38	75	VII, VIII	XVII, XVIII	5/6	37	45	4	XVII–XX	XXVII–XXIV
28	35	78	VII, VIII	XVII, XVIII	5/6	39	44	4	XVII–XIX	XXVII–XXV

All the key morphological characters of the holotype and paratype specimens are given in Table 5.

Variation: The holotype measures 47 mm body length with 77 segments and the first dorsal pore located at 5/6; the twenty eight paratypes range in size between 35–47 mm (39.75±4.27 mm) body length with 52–78 segments, and first dorsal pore at 4/5 (8 samples) or 5/6 (20 samples) (Table 5).

Type locality: Srinan National Park, Nan province, Thailand, 18°22'11.1"N, 100°50'23.2"E, 607 meters elevation (30th September 2010).

Etymology: This species was named after the type locality Srinan National Park.

Type material: The holotype (CUMZ 3210) and 25 paratypes (CUMZ 3211) are deposited in Chulalongkorn University, Museum of Zoology. Another five paratypes will be deposited in the Biozentrum Grindel und Zoologisches Museum, Hamburg, Germany (UHH), and four paratypes in the Natural History Museum, London (NHM).

Habitat: Found in the top soil at about 10 cm depth, the soil surface covered with leaf litters of deciduous forest. The soil was carefully dug close to the castes.

Diagnosis: *Amynthas srinan* sp. n. is the smallest *Amynthas* ever collected in Thailand. Male pores on distinct round porophores, genital markings paired near mid ventral of VII, VIII, XVII and XVIII; each with genital marking glands. Each spermathecae consists of a kidney-shaped ampulla and an oval shaped diverticulum. Testes sacs ventrally joined, intestinal origin XV, intestinal caeca simple, first dorsal pores at 4/5 or 5/6.

Remarks: *Amynthas srinan* sp. n., along with *A. exiguus exiguus* and *A. tontong* sp. n., is one of if not the smallest *Amynthas* recorded so far. It has external characteristics which are easily seen in both newly collected and preserved materials. Compared with the two other closely related species from Laos, *A. chandyi* and *A. namphouinensis*, which belong in the same *zebrus*-group, *A. chandyi* is very similar in appearance to *A. srinan* sp. n. However, they clearly differ in certain specific details of their significant characters, such as the distance between the mp which in *A. srinan* sp. n. is 1.5 mm for holotype and ranged from 1.5–2.0 mm (1.41±4.27 mm), while in *A. chandyi* this ranged from 1.5–2.4 mm. The distance between the male pores as a fraction of the estimated circumference of the 18th segment is 0.24–0.30 in *A. srinan* sp. n., and 0.14–0.32 in *A. chandyi*. This is not convincing as a diagnostic difference, because there is significant overlap with the highly variable *A. chandyi*. In addition, although genital markings are clearly observed in both *A. chandyi* and *A. srinan* sp. n. on the sc and mp areas, *A. srinan* sp. n. has a much larger number and different arrangement of such markings. The distance between pairs of sp is quite similar, being 1.5–2.0 mm (1.34±2.31mm) in *A. srinan* sp. n. and 1.2–1.5 mm in *A. chandyi*.

Discussion

The genus *Amynthas* is widely distributed in the Asian continent, where it is one of the dominant genera. In Thailand it occurs in various types of lowland forest habitats, dry evergreen, moist evergreen, deciduous and limestone forests, encompassing diverse soil pH values, from acidic to alkali soils (Chantaravisoot, 2007) and from clay to muddy sand substrates (Kosavititkul, 2005; Somniyam, 2008; Blakemore et al., 2007). The current four new species described here were all are found in one area (Nan province) but the four habitat types were quite diverse all the same. *Amynthas phatubensis* sp. n. was found in a limestone area with a mild alkali substrate (pH 7.5–8) of a clay loam structure, whilst the other three species were found in harder sandy clay substrates. The four new species are broadly similar (and so potentially related) to the two species described from Laos, *A. chandyi* and *A. namphouinensis,* but differ in both the external and internal morphological characteristics. The geographic structures of Luang Prabang Mountain and Phi Pan Nam Mountain ranges are important barriers for species from both the Thai (Nan province) and Laos side (Xayabouli province) and may have played an important part in their speciation. In addition, the Laos species live at a higher altitude than the current new described species from Thailand, and such selective adaptations may facilitate their morphological discrimination.

The four new species range in size, with respect to other *Amynthas* members, from moderate to very small, of which *A. phatubensis* sp. n. is the longest. The other three species are almost the same size and close to the two Laotian species, as shown in Table 6. However, the spermathecae (sc) and genital marking locations of the four new species are clearly different from the two closely related Laos species. The four new *Amynthas* species described here belong to the *zebrus*-group, as defined by Sims and Easton (1972),in which the spermathecal pores are located on segment 7/8. The size of these four species, relative to other *Amynthas* species, varied from small to medium, ranging from 35 to 148 mm in body length and having from 52 to 114 segments. The first dorsal pore in three of the four species described here, and most of the samples of the fourth species (*A. srinan* sp. n.), is located on intersegmental furrow 5/6, but with some samples of *A. srinan* sp. n. showing the first dorsal pore at 4/5.

Amynthas phatubensis sp. n. is the only species that lives in limestone habitats in leaf litter and also in shallow mild alkali topsoil. The soil humidity can be quite low and is of a clay loam structure. The other three species are smaller in size and were found in almost harder, muddy sandy clay substrates. *Amynthas tontong* sp. n. lives in deeper soil of a high humidity around waterfalls. *Amynthas borealis* sp. n. and *A. srinan* sp. n. are found in deciduous forests, which have mostly been modified as agricultural fields. The soil is drier and harder. The genital marking glands of *A. phatubensis* sp. n. and *A. srinan* sp. n. are distinct from other two species (Table 6 and Figs 2–5), whilst *A. tontong* sp. n. show two postclitellar genital markings that are absent in *A. borealis* (Figs 3 and 4) The diagnostic differences are shown in the dichotomous key to the sixteen Thai and two Laotian *Amynthas* species, below.

The *zebrus*-group is composed of eleven nominal species: *Metaphire hilgendorfi* (Michaelsen, 1892), *A. palmosus* (Chen, 1946), *A. magnipapillatus* (Qui and Wang, 1992), *A. zebrus* (Benham, 1896), *A. culminus* Michaelsen, 1899, *A. principalis* (Michaelsen, 1932), *A. xuongmontis* (Thai & Samphon, 1990), *A. fasciculus* (Qui,

Table 6. Morphological characteristics for between these four new species and two know species from Laos

Characters	*A. phatubensis* sp. n.	*A. tontong* sp. n.	*A. borealis* sp. n.	*A. srinan* sp. n.	*A. namphouinensis*	*A. chandyi*
Body length (mm)	80–148	39–53	42–54	35–47	63–92	29–58
Number of segments	85–112	71–80	78–89	56–77	92–94	48–52
First dorsal pore	5/6	5/6	5/6	4/5, 5/6	4/5, 5/6, 6/7	5/6
Setae number						
VII	51–64	41–46	39–54	36–45	52–61	44–54
XX	58–68	52–55	40–52	42–49	53–58	44–57
between male pores	9–15	0	0	4–6	0–7	0–7
Preclitellar genital markings						
VII	2	0	0	2	0	1–2
VIII	1–7	0	0	2	0	1–2
IX	0–1	0	0	0	0	0
Postclitellar genital markings						
XVII	0–2	0	0	2	2	1
XVIII	6–12	2	0	2	0	3
XIX	0–1	0	0	0	4	1
XX	0–1	0	0	0	0	1
Prostate glands	XVII–XX	XVII–XX	XVII–XX	XVII–XX	XVII–XIX	XVI–XXI
Genital marking glands	sessile at VII, VIII	Absent	absent	stalked	sessile at XVII–XIX	absent
Intestinal caeca	simple, XXVII–XXIII	simple, XXVII–XXV	simple, XXVII–XXV	simple, XXVII–XXII	simple, XXVII–XXIV	simple, XXVII–XXIV

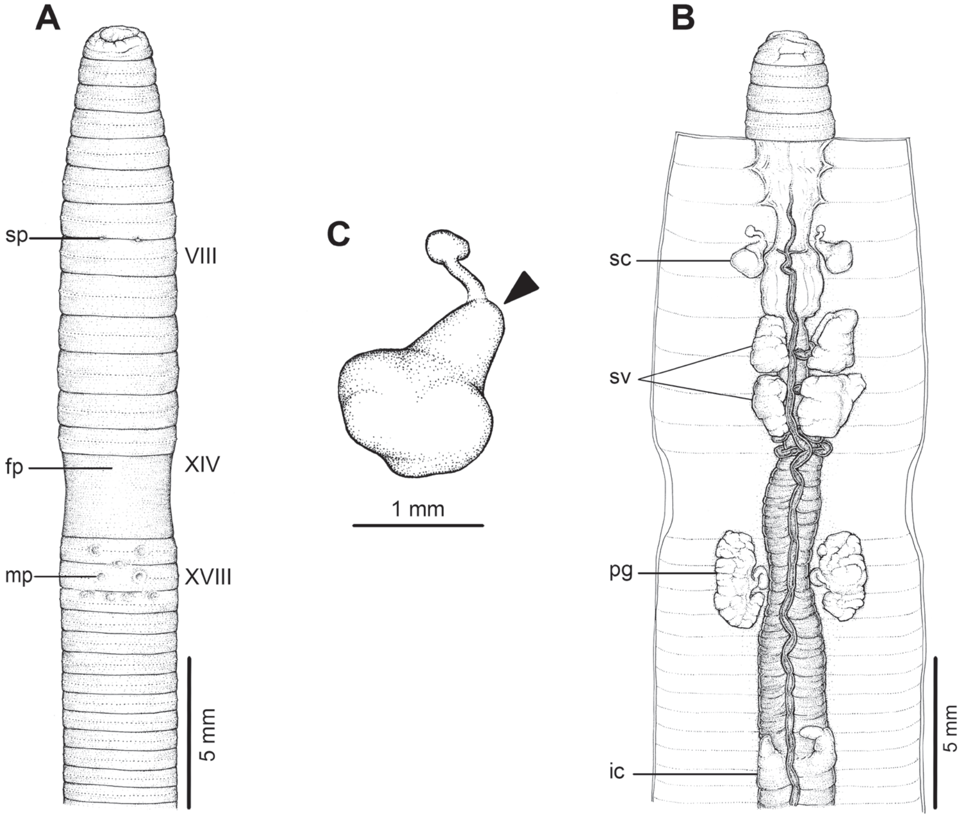

Figure 6. External and internal morphology of holotype (BDNUL 0001) of *Amynthas namphouinensis* Hong, 2008 **A** External ventral view, **B** internal dorsal view and **C** spermatheca, and black arrow indicates the connection of the spermatheca and spermathecal pore.

Wang & Wang, 1993), *A. heaneyi* James, 2004, *A. namphouinensis* Hong, 2008 and *A. chandyi* Hong, 2008. Within the *zebrus*-group, the first three species show manicate intestinal caeca, while the current newly described four species have simple finger-shaped intestinal caeca. The three latter nominal species are longer in body length (200–300 mm) compared with the size of these four new species which ranged from 35–148 mm. *Amynthas heaneyi* can be distinguished by its proandric character (James, 2004), while the four new described species are holandric. *Amynthas fasciculus* has coiled and kinked spermathecae, whereas *A. phatubensis* sp. n. has large ovate ampulla, *A. tontong* sp. n. has thumb shaped ampulla, *A. borealis* sp. n. has sac-shape ampulla, and *A. srinan* sp. n. has oval to kidney-shaped ampulla. *Amynthas xuongmontis* clearly differs from these four new species in the genital marking located on XVIII, whereas located on VII, VIII, XVII, XVIII in *A. phatubensis* sp. n., located between 18/19 in *A. tontong* sp. n., absent in *A. borealis* sp. n. and located on VII, VIII, XVII, XVIII in *A. srinan* sp. n.

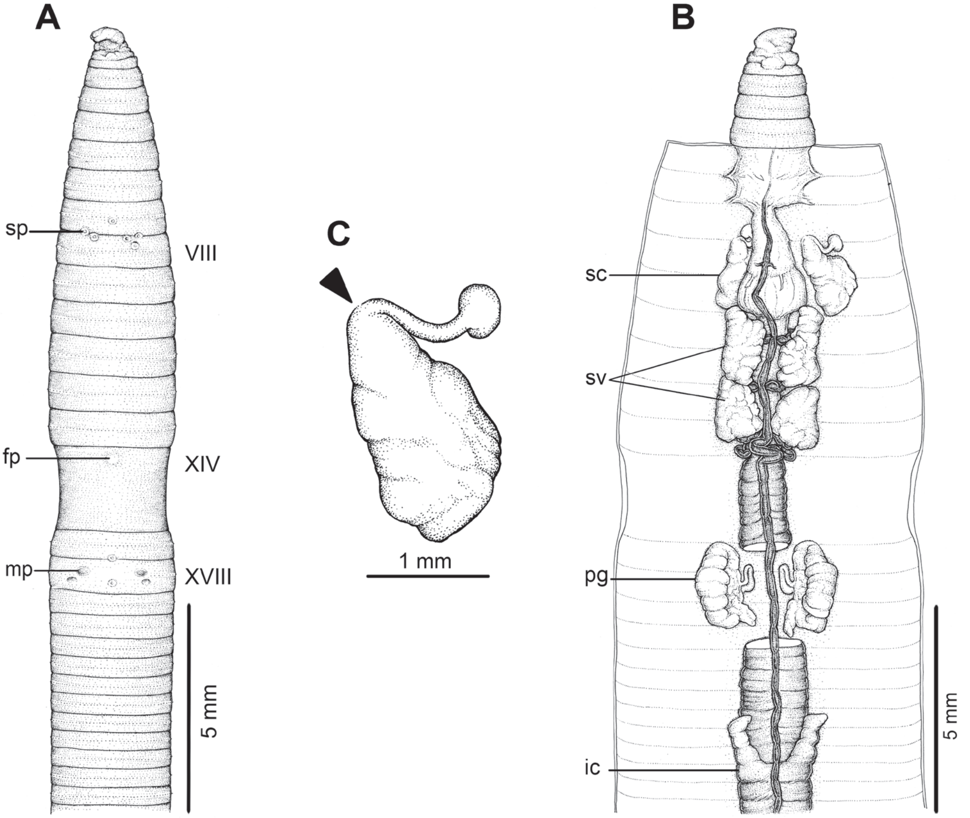

Figure 7. External and internal morphology of holotype (BDNUL 0002) of *Amynthas chandyi* Hong, 2008 **A** External ventral view, **B** internal dorsal view and **C** spermatheca, and black arrow indicates the connection of the spermatheca and spermathecal pore.

Key to Thai and two Laos species of *Amynthas*

1	First spermathecal pores at 5/6	**2**
–	First spermathecal pores after 5/6	**12**
2	Two pairs of spermathecal pores	***A. morrisi***
–	More than two pairs of spermathecal pores	**3**
3	Three pairs of spermathecal pores	**4**
–	More than three pairs of spermathecal pores	**6**
4	Genital markings absent	***A. defecta***
–	Genital markings present	**5**
5	Genital markings clustered on XVIII	***A. gracilis***
–	Genital markings transverse rows on XVII, XVIII, XIX	***A. papulosus***
6	Genital markings absent	**7**
–	Genital markings present	**8**
7	Body length 1 meter or more	***A. mekongianus***

– Body length less than 300 mm..***A. alexandri***

8 Genital marking glands absent...**9**

– Genital marking glands present...**10**

9 Genital markings located on 17/18, 18/19...................***A. exiguus austrinus***

– Genital markings located on VII, VIII, XIX, XX ....***A. exiguus exiguus***

10 Intestinal caeca, simple **11**

– Intestinal caeca, manicate.......................................***A. manicatus decorosus***

11 Genital markings, paired at 18/19, 19/20, 20/21..........***A. longicauliculatus***

– Genital markings, three trios at 18/19, 19/20, 20/21.................***A. comptus***

12 First spermathecal pores at 6/7...**13**

– First spermathecal pores after 6/7..**14**

13 Genital markings located on 17/18, 18/19...................................***A. fucosus***

– Genital marking located on XVIII ....***A. siam***

14 Body length more than 200 mm...***A. hupbonensis***

– Body length less than 200 mm...**15**

15 Genital markings absent ....***A. borealis sp. n.***

– Genital markings present **16**

16 Preclitellar genital markings absent **17**

– Preclitellar genital markings present **18**

17 Genital marking glands absent...***A. tontong sp. n.***

– Genital marking glands present.....................................***A. namphouinensis***

18 Genital marking glands absent..***A. chandyi***

– Genital marking glands, present...**19**

19 Genital marking glands, sessile....................................***A. phatubensis* sp. n.**

– Genital marking glands, stalked...***A. srinan* sp. n.**

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Appendix 1.

DNA barcode sequences for *A. phatubensis* sp. n. and *A. tontong* sp. n. Positions with variable base are indicated by the appropriate ambiguity code: Y= C or T, R= A or G, K= G or T, M= A or C.

The primer sets used, LCO1490 and HCO2198, amplify a 658 bp fragment of the COI gene in a wide range of invertebrate taxa (Folmer et al 1994):

LCO1490: 5’-GGTCAACAAATCATAAAGATATTGG-3’
HCO2198: 5’-TAAACTTCAGGGTGACCAAAAAATCA-3’

Consensus of 8 sequences of *Amynthas phatubensis* sp. n. **Paratype** CUMZ 3212, GenBank Accession No. HM901031-HM901038.

AACCCTATATTTCATTTTAGGTATTTGAGCCGGTATGATTGGATCTGGAATAAGCCTACTYATCCGAATTGARTTGAGCCAACCTGGATCCTTCCTAGGCAGAGATCAGCTATACAATACCATTGTTACAGCTCATGCATTCTTAATAATYTTCTTTTTAGTTATACCCGTATTTATTGGGGGTTTTGGAAACTGATTAYKACCACTTATACTTGGRGCGCCAGATATRGCCTTTCCYCGACTAAACAACATAAGATTCTGATTGCTTCCTCCRTCRCTTATTCTATTAGTAAGCTCTGCGGCCGTRGAAAAGGGGGCYGGCACTGGATGAACTGTTTACCCMCCCCTAGCTAGAAATGTRGCCCACGCAGGGCCTTCAGTAGATTTAGCTATTTTCTCACTTCATTTAGCAGGAGCTTCATCTATTTTAGGGGCAATTAATTTCATTACAACTGTAATTAATATGCGATGATCCGGACTACGTCTAGAGCGTATCCCACTATTTGTATGGGCCGTRGTTATCACAGTAGTACTATTATTACTTTCCCTRCCTGTATTAGCAGGGGCTATCACTATACTACTAACTGAYCGTAATCTAAACACATCATTTTTTGATCCTGCTGGGGGCGGCGACCCCATTCTATATCAACACCTA

Consensus of 3 sequences of *Amynthas tontong* sp. n. **Paratype** CUMZ 3207, GenBank Accession No. HQ562073-HQ562076.

AACCCTATACTTCATTTTAGGAATTTGAGCTGGAATAATTGGAGCAGGAATAAGACTCCTTATTCGAATTGAGYTAAGACAGCCCGGATCATTCCTAGGAAGYGATCAACTATACAATACCATTGTTACAGCCCATGCATTCTTAATAATTTTCTTCCTRGTAATGCCAGTATTTATTGGGGGCTTTGGAAATTGATTACTTCCACTAATGTTGGGGGCCCCTGACATAGCTTTCCCACGACTAAATAATATGAGATTTTGACTACTTCCACCATCATTAATCCTTTTAGTTAGATCCGCRGCCGTTGAAAAAGGTGCGGGGACAGGATGAACTGTATACCCACCACTAGCAAGGAACATTGCCCATGCTGGCCCATCTGTAGATTTAGCAATTTTCTCACTACACTTGGCGGGGGCATCCTCAATCCTGGGGGCTATTAACTTCATTACCACAGTAATTAATATGCGATGATCTGGGCTGCGCTTAGAACGAATCCCCCTATTTGTATGAGCTGTAGTAATTACAGTAGTACTCCTACTACTATCTTTGCCCGTGCTGGCGGGAGCCATTACAATACTCTTAACAGATCGAAATCTTAATACATCATTCTTCGACCCTGCTGGCGGGGGCGACCCTATTCTATACCAGCACCTG

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The larva of *Eustra* (Coleoptera, Paussinae, Ozaenini): a facultative associate of ants

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Abstract

Larvae of the ground beetle genus *Eustra* Schmidt-Goebel are described and illustrated for the first time and some biological notes are reported. One specimen of an unknown *Eustra* species was collected while excavating a nest of the ant *Pachycondyla javana* Mayr, in Taiwan, which is the first report of a paussine associated with a member of the ant subfamily Ponerinae. Several larvae and adults of a second species, *E. chinensis* Bänninger, were collected in Shanghai under bark with no association with ants. First instar larvae of the latter species were also reared in the lab. The occurrence of larvae of the genus *Eustra* both inside and outside ant nests, together with a report of adults collected inside a nest in Taiwan, suggests that members of this genus may be facultative predators or facultative symbionts of ants, an attribute that has never been reported for this genus. The larvae of *Eustra* show several unique features, including a peculiar bidentate mandibular apex, an extremely long galea, one of two tarsal claws greatly reduced, abdominal setae (including those of terminal disk) elongate and clavate at apex, urogomphi wide and flattened, and inflated sensilla S-I. Larvae were studied by both optical and scanning electron microscopy, their morphological features are compared with those of other described Paussinae larvae, and their potential phylogenetic and functional significance are discussed.

Keywords

flanged bombardier beetles, myrmecophily, systematics, larvae, Southeast Asia

Introduction

Eustra Schmidt-Goebel is an ozaenine genus (Carabidae: Paussinae) containing twenty-two species (reviewed by Deuve 2001). Adults in this Southeast Asian genus have the smallest body size of all members of the subfamily Paussinae. Many *Eustra* species live in caves and exhibit typical structural adaptations to a troglobitic life, including loss of pigmentation, loss of eyes, and long, delicate appendages. Other species are not cave-dwelling, but rather they have been collected in microhabitats typical of other ozaenines including under rocks and under bark. Recently larvae of two species of *Eustra* were collected in the field. Both adults and larvae of *Eustra chinensis* Bänninger were collected in Shanghai while they were hibernating in rotting wood and a single larva of an unidentified species of *Eustra* was collected during the excavation of nests of the ant *Pachycondyla javana* Mayr in Taiwan, suggesting for the first time that at least some species of *Eustra* are facultatively associated with ants (Moore 2006).

Many different animals, especially arthropods, profit from a facultative or obligate association with ants (myrmecophily), bypassing the behavioral and chemical defenses of the hosts and adapting to the peculiar environmental conditions of the nests. Since myrmecophiles are rare and live in concealed environments, our knowledge of their behavior is sparse, and most of the information we do have has been inferred from structural features of adults and larvae (Di Giulio and Moore 2004; Di Giulio et al. 2011). The Paussinae, commonly known as flanged bombardier beetles, are a good model taxon to study the evolution of myrmecophily in beetles, since members of this ground beetle subfamily have different degrees of associations with ants, ranging from apparently none to obligate myrmecophiles (see Geiselhardt et al. 2007 and references therein). As far as we know all members of the tribes Protopaussini and Paussini are myrmecophilous, at least during the larval stage, and their associations with ants have either been directly observed in the field or deduced from their remarkable structural adaptations. Most of these species associate with members of the ant subfamilies Formicinae and Myrmicinae.

In general, very little is known about the behaviour of the ozaenines (Di Giulio and Vigna Taglianti 2001; Moore and Di Giulio 2006; Moore 2008). Like most ground beetles, they are usually found under stones, bark, and rotting wood and they are night-active predators on other arthropods. Ozaenine larvae are known for only nine species in four genera (*Itamus*, *Sphaerostylus*, *Pachyteles* and *Physea*) (see Di Giulio and Moore 2004). They all have a terminal disk composed of modified abdominal tergites and urogomphi, which is a synapomorphy for the subfamily (Bousquet 1986). Unlike the physogastric myrmecophilous larvae of the tribe Paussini which use their round terminal disk as a glandular symphilous organ (Oberprieler 1985; Bousquet 1986; Luna de Carvalho 1989; Di Giulio and Moore 2004; Di Giulio et al. 2011), free-living larvae of Metriini, Mystropomini and Ozaenini use their terminal disk as a door to close the galleries they construct in rotten wood, humid earth or sandy riverbanks, and they use the moveable components of the terminal disk to trap their prey (Costa et al. 1988; Di Giulio and Vigna Taglianti 2001), seizing them with their sharp mandibles through a backward spring-like movement. This specialized feeding strategy allows these delicate larvae to feed on fast moving invertebrates and to occasionally feed on ants. It is likely that many non-myrmecophilous members of the subfamily Paussinae facultatively feed on ants, as has been demonstrated in the tribe Metriini (Moore and Di Giulio 2008). We hypothesize that myrmecophagy may be a preadaptation for myrmecophily.

Members of the ozaenine genus *Physea* Brullé are known to live inside the nests of the Neotropical leafcutting ants, *Atta*, and both larvae and adults have structural adaptations for this lifestyle (Eidmann 1937, Di Giulio et al. 2003). Recently adults of other ozaenine species have been found inside *Atta* nests including adults of *Tachypeles moretianus* Deuve and *Serratozaena paraphysea* Deuve (Moore 2008). Based on structural features of adults, myrmecophily has also been hypothesized for the Southeast Asian species *Dhanya mulu* Stork (Stork 1985), and the South and Central American genera *Ozaena* Olivier and *Platycerozaena* Bänninger (Ball and McCleve 1990). Larval specimens of the Malagasy species *Sphaerostylus goryi* (Laporte de Castelnau) were recently collected both in rotten wood with ants and in leaf litter without apparent association with ants (WM, personal observations). The discovery of an *Eustra* larva inside a *Pachycondyla javana* nest in Taiwan is the only report of a paussine associated with a member of the ant subfamily Ponerinae (Moore 2006). That *Eustra* larvae have been collected both inside and outside of ant nests suggests the possibility that they are at least facultatively associated with ants. In addition, a report of adults of *Eustra* sp. collected inside an ant nest in Taiwan was posted on the Internet (http://nc.kl.edu.tw/bbs/showthread.php?t=653&page=9). These findings suggest that more ozaenine taxa may be facultative or obligate myrmecophiles, even those without evident structural adaptations, and they suggest that myrmecophily has evolved multiple times during the evolution of in Paussinae (Moore 2006; Moore et al. 2010).

In this paper we: (1) present biological information about the habitats and behaviors of *E. chinensis* and the *Eustra* species from Taiwan observed in nature and in captivity; (2) describe and illustrate these larvae; (3) discuss the functional significance of several unique characteristics of the genus; and (4) compare them to other described paussine larvae.

Methods

Material described

(1) *Eustra chinensis* Bänninger, 1949. Twenty-five adults and several larvae were collected in Shanghai on February 9, 2009 and April 6, 2008. They were found hibernating together in the soft, rotten wood of bristly locust (*Robinia hispida* Linnaeus, 1767) and weeping willow (*Salix babylonica* Linnaeus, 1753). Adults and larvae can be found in Shanghai throughout the year. They overwinter as both adults and larvae (all larval instars), from November to April. Presumably, while these larvae are overwintering they do not feed. In captivity, a third instar larva overwintered without food for more

than six months. During this time they did not close the opening of their galleries with their terminal disks, as they do to facilitate feeding during the spring and summer (as described for other ozaenine larvae, see Costa et al. 1988; Di Giulio and Vigna Taglianti 2001; Moore and Di Giulio 2006).

(2) *Eustra sp*. A single third instar larva was collected in northern Taiwan (Shanshya [sic]) by Gustav Tzh-wei Chen on 9.IX.2003 while excavating a nest of *Pachycondyla javana* Mayr (Hymenoptera, Formicidae, Ponerinae). The specimen was identified as belonging to the genus *Eustra,* by a phylogenetic analysis of molecular sequence data obtained from this specimen and from sixty other members of the subfamily Paussinae, including other members of the genus *Eustra*.

Rearing conditions

Larvae of *E. chinensis* were reared in captivity, where ambient conditions (*e.g.*, temperature, light and humidity) were similar to natural conditions outdoors. Five larvae of each instar were reared in 2 ml centrifuge tubes. Other larvae were reared in a plastic box (18 cm × 11 cm × 12 cm) with the field-collected rotten wood. All larvae were fed springtails once a month.

Morphological analysis

Prior to preparing them for microscopy, larvae were drawn by a stereomicroscope Olympus SZX16 equipped with drawing tube. One specimen of each instar of *Eustra chinensis*, and the single specimen from Taiwan were rehydrated, cleared in 10% KOH, transferred in hot lactic acid, dehydrated through a series of EtOH baths of increasing concentration (10-20-50-70-90-95-100%), left overnight in a clove oil bath, and mounted on slides with Canada balsam. These specimens were studied and illustrated by using a light microscope Olympus BX51 equipped with drawing tube. Another first instar specimen was dehydrated through a series of EtOH baths of increasing concentration (70-80-90-95-100%), critical point dried (Bal-Tec CPD 030), mounted on a stub (by using self adhesive carbon disks), sputtered with gold (Emitech k550 sputter coater), and observed with Philips XL30 scanning electron microscope and FEI Dualbeam FIB/SEM Helios Nanolab (L.I.M.E. laboratory, University 'Roma Tre', Rome). In this paper, the general terminology of larval structures follows Lawrence (1991). Notation of primary setae and pores follows the system of Bousquet and Goulet (1984), modified for *Metrius contractus* (Bousquet 1986). Because some of the sensilla on the abdomen and terminal disk of *Eustra* are homologous to those recognized in *Metrius contractus* (sensilla S-I to S-V) (Bousquet 1986), *Pachyteles* spp. (sensilla S-I to S-VII) (Di Giulio et al. 2000), and *Arthropterus* sp. (sensilla S-I to S-VIII) (Di Giulio and Moore 2004), we adopt here the same nomenclature used by these authors. Notation of microsculpture follows Harris (1979). An asterisk (*) following a coded seta indicates that the homology between the structure on the *Eustra* larvae and the corresponding code is questionable.

Results

Eustra larval morphology

Generic diagnosis. Body length very small as compared with other Paussinae (1.75mm, first instars); antenna 3-jointed (II+III fused); mandible apically bidentate, with sub-basal retinaculum, ental margin of retinaculum with additional small sub-basal tooth; galea extremely long and apically sharp, distinctly longer than maxillary palp and lacinia; maxillary palpomere 3-jointed (II+III fused); claws of very different size, smaller claw obsolescent; hypopleurite VI with ventrolateral, elongate digitiform protuberance, tipped by strong spine-like seta; most sternal and pleural setae of the abdomen elongate and clavate at apex; lateral plates of terminal disk thin and wing-like, pointed at apex, with dorsal margin straight and ventral margin curved; urogomphi flattened, wider and longer than dorsal plates, composed by 7 short triangular lobes, acute at apex, separated by V-shaped incisures of different depths; lobe X present between C and E2; lobe E1 divided into E1a and E1b; peculiar mushroom-like inflated sensilla S-I of different length present on surface of plates and urogomphi; sensilla S-II of two different types, alternate on dorsal plates and urogomphi: (1) very long and stick-like, pointed at apex; (2) short and clavate at tip; terminal disk covered with peculiar hairy microsculpture.

Eustra chinensis first instar larva

Habitus and coloration. Body soft, whitish, weakly sclerotized, not physogastric; abdomen flattened, bellows-like, contracted dorsally elevating the large terminal disk; terminal disk, cephalic capsule and mouthparts well sclerotized, yellowish to light brown; mandibles, laciniae, anterior margin of frontal sclerite, egg-bursters and claws thickly sclerotized and reddish brown.

Microsculpture. Cephalic capsule, mouthparts, thoracic tergites and legs smooth, without or with only sparse, pointed microsculpture (Figs 2, 5a, 5b); anterior margin of frontoclypeolabrale to adnasalia strongly denticulate at sides of median prominence, resulting in a serrate anterior edge (Figs 1a, 2a); anterior frontal keel smooth; basal third of prementum (Figs 1f, 2a, 3f) and stipes (Figs 1e, 2a, 3f) with pointed microsculpture on dorsal surface; membranous areas of the body and sclerites of the abdomen rugulose to rugose (Figs 5a, 5c-f), with pointed or multi-pointed sculpticells, sparse near the setae, longer on epipleurites I-VII; dorsal surface of dorsal plates, basal part of lateral plates and ventral surface of urogomphi covered by transverse rows of 2-6 spines (2-3 µm long), regularly spaced every 3-6 µm (Fig. 7d); surface of terminal disk

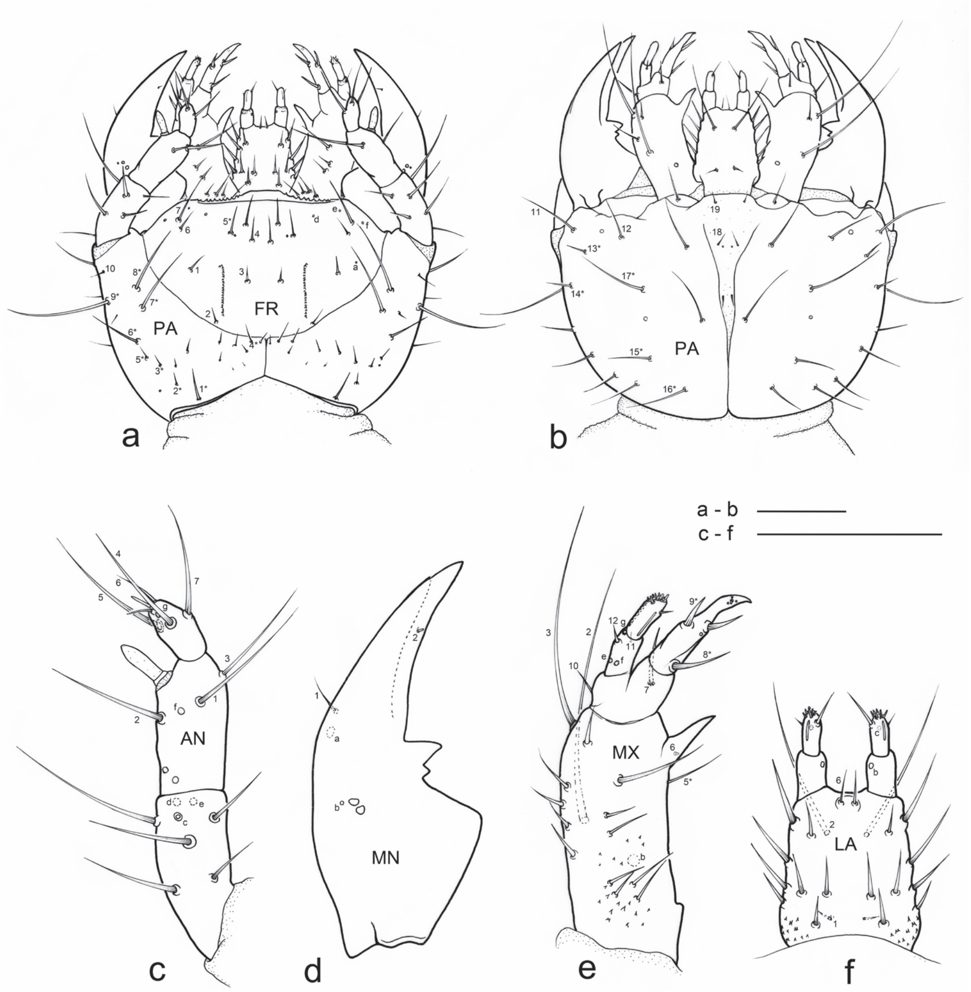

Figure 1. *Eustra chinensis* first instar larva: line drawings of **a** head, dorsal view **b** head, ventral view **c** left antenna, dorsal view **d** left mandible, dorsal view **e** left maxilla, dorsal view **f** labium, dorsal view. Scale bars: 0.1 mm.

(Fig. 7) thickly covered by a peculiar hairy microsculpture; pygidium, with pointed to multi-pointed microsculpture.

Chaetotaxy. Frontoclypeolabrum (Figs 1a, 2a-c) without additional setae; $FR_{1-4,6-9}$ easily distinguished (Fig. 1a); medial prominence of frontoclypeolabrum with 2 minute spine-like setae on dorsal surface (Fig. 2b); FR_b absent; several minute filiform sensilla (Fig. 2b) expanded at apex present on anterior part of frontale (Figs 2e-f). Parietale (Figs 1a, 2c) with several small additional setae irregularly positioned mesodorsally, and longer additional setae placed ventrally; some setae of parietale possibly homologous to the ancestral pattern are tentatively assigned in Fig. 1a. Antennomere I (Figs 1c, 2c) with 5 dorsolateral additional setae; $AN_{a,b}$ absent; III with AN_1 and AN_f displaced apically (Fig. 1c). Mandibles (Fig. 1d) with two large additional pores mesodorsally. Setal group gMX on stipes composed of about 10 setae (Fig. 1e); MX_6 very small, dorsal and subbasal on lacinia; galeomere II with one additional seta on ental side and a subapical, dorsal sensorial area (composed of 3 dome-like and 1 longer medial sensilla) (Fig. 3c); maxillary palpomere IV with 1 small additional seta on ental side, 2 longitudinal subapical digitiform sensilla (Fig. 3e) and apical sensorial area composed of several papillae. Prementum (Figs 1f, 3f) with about 10 additional setae on lateral and dorsal surface, $LA_{3,4,5}$ not clearly identifiable; seta LA_1 close to the midline; LA_a absent, LA_c subapical; labial palpomere II with 2 additional setae, 1 dorsal, medially directed and 1 small ventrolateral, 2 longitudinal subapical digitiform sensilla and apical sensorial area composed of several papillae. Pro-, meso- and metanotum (Figs 4a, 5a) with about 25 setae each (identification not possible). Coxa with about 20 setae; trochanter with spiniform setae present mostly on ventral side, including a long TR4; TR8 about as long as TR4 but thinner and more flexible. Meso- and metasternum with MS4 long. Abdominal tergites I-VII (Fig. 4c) with 4 setae on each side. Tergal side of dorsal and lateral plates of terminal disk (Figs 4c, 7b) with stiff pointed setae (sensilla S-VII) of various sizes, with cylindrical bases protruding from the plates: about 14 on each dorsal plate (epipleurite IX + tergite VIII) and about 3 on each lateral plate (epipleurite VIII); distal margin of each dorsal plate with about 12 elongated, straight and deeply corrugated sensilla S-II, of two different sizes and shapes (Fig. 6a) alternately placed: type 1 extremely long (about double than type 2), stick-like, with sharp tip; type 2 thinner than 1 and distinctly clavate at apex; inner edge of each dorsal plate (Fig. 6a) with 2-3 S-II type 2 obliquely directed, increasing in size from base to apex; margin of each lateral plate with 8 sensilla S-II, 5 of type 1; caudal side of the terminal disk with numerous sensilla S-I (Figs 4d, 6a) sparsely distributed: 25-30 S-I on each dorsal plate and about 1-4 on each lateral plate. Epipleurites (Figs. 4c-d, 5c-d) of abdominal segment I without setae, II-V with one elongate sensillum S-II (type 2) each, VI-VII with several setae and S-II type 2. Sternal area of segment I with small simple setae, II-VI with elongate sensilla S-II type 2, VII with simple elongate setae (except for one, see Fig. 4d). Urogomphi (Figs 6a, 7a, c) with many S-I (about 40), mainly on dorsal surface and at margins of branches; branches A, C, X and E1b with S-II type 2 (Fig. 7a), B, E2, E1a with apical long S-II type 1 (Fig. 7a, f). Pygidium without setae (Fig.7a).

Head. Cephalic capsule (Figs 1a-b, 2a-c) strongly transverse (width/length ratio = 1.86), hyperprognathous, rounded laterally, regularly tapered at basal half into a distinct neck; maximum width at antennal insertions about twice as wide as occipital foramen. Frontoclypeolabrum (Figs 1a, 2a,c) strongly transverse (width/length ratio = 1.64), with surface medially convex and anterolaterally concave; basal stem of epicranial suture short, anterior frontal arms only slightly sinuate; egg-bursters (Fig. 2d) composed of two longitudinal, multispinulate carinae, each consisting of about 20 forwardly directed teeth; carinae parallel, about one third the length of frontoclypeolabrum, widely separated, placed between FR1 and FR3. Anterior margin of frontoclypeolabrum (Figs 1a, 2a-b) double-edged: dorsal edge smooth, slightly convex, form-

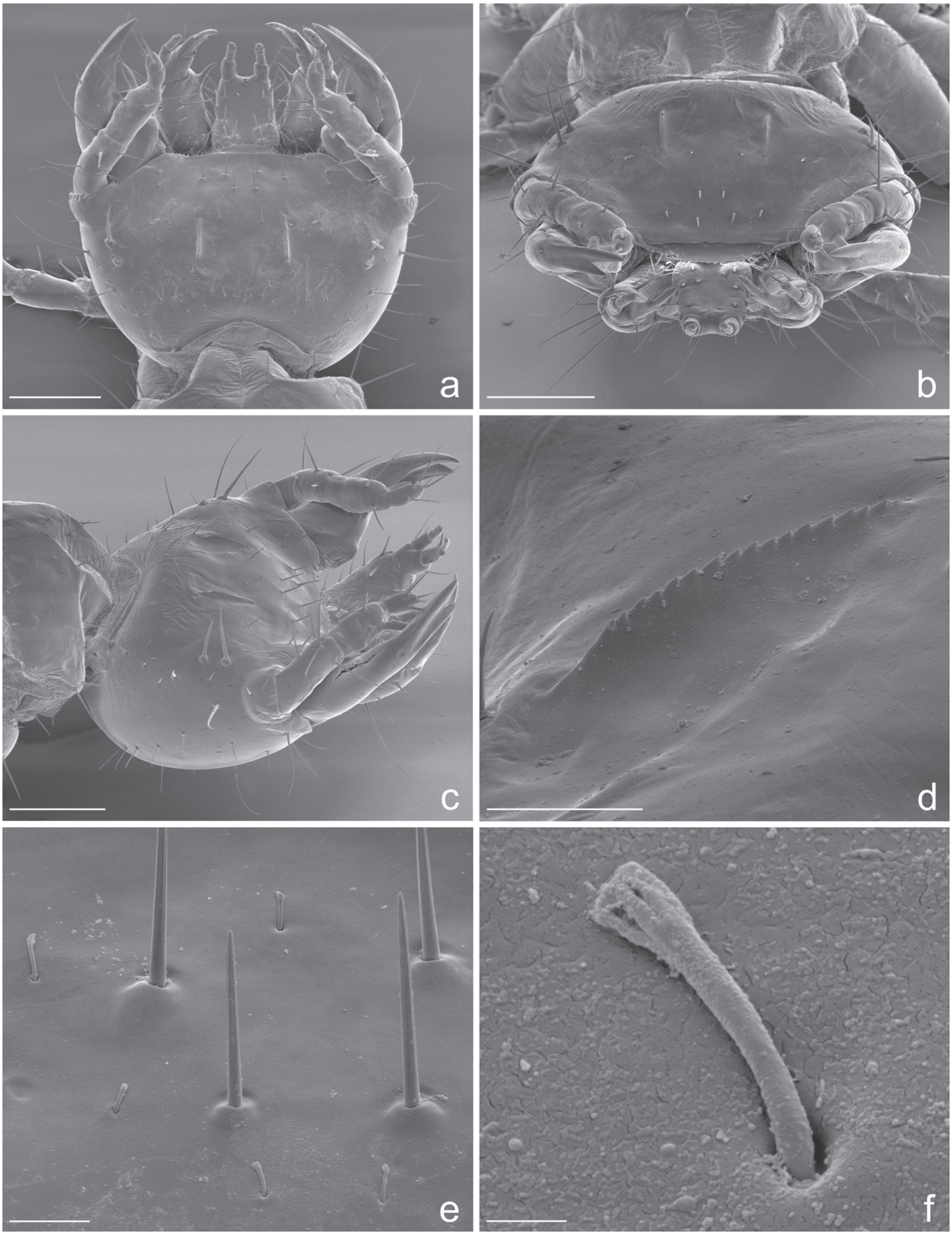

Figure 2. *Eustra chinensis* first instar larva: SEM micrographs of **a** head, dorsal view **b** head, frontal view **c** head, dorsolateral oblique view **d** left egg-burster, right dorsolateral oblique view **e** basal setae of frontoclypeolabrale, with filiform sensilla, dorsal view **f** close-up of a filiform sensillum of frontoclypeolabrale. Scale bars: **a**, **b**, **c** = 100 µm; **d** = 20 µm; **e** = 10 µm; **f** = 1 µm.

ing a transverse keel (see Di Giulio et al. 2003 and Di Giulio and Moore, 2004 for a discussion on the homology) extended to the adnasalia, ventral edge strongly serrate laterally, medially produced into a wide subrectangular labral tooth (labral spine *sensu* Beutel 1992); adnasalia slightly rounded and slightly protruding. Parietale (Figs 1a-b, 2c) without stemmata; ocular and cervical grooves absent; ventral walls of parietale medially fused into a complete gular suture (Fig. 1b). Antennae (Figs 1a, 2a) strongly directed mesad, 3-jointed; antennomere I (first joint) about as long as II+III (second joint) and twice as long as IV (third joint); sensorial appendage (Figs 1c, 3a) elongate, bullet-like, slightly shorter than IV, laterally positioned at apex of III. Mandibles (Figs 1d, 3b) stout, sickle-shaped, about 2 times as long as wide at base, regularly curved along lateral margin; apex sharply bidentate, lower tooth smaller than upper and distinctly divergent; penicillus absent; terebra slightly convex beyond retinaculum, then concave to apex; retinaculum small sub-triangular, sub-basal in position, postero-medially directed; anterior margin rounded and convex, posterior margin straight, with sub-basal tooth. Maxilla (Figs 1e, 3c) with undivided cardo, subrectangular stipes, 3-jointed palp, 2-jointed galea and 1-jointed lacinia. Stipes distinctly curved inward, about 3 times as long as wide at base; small tooth-like protuberance present subbasally on the ental side of stipes. Maxillary palpi short; palpomere I wide and subconical, medially fused with basal galeomere; II fused with III forming a unique second joint; IV (third joint) elongate, digitiform, about as long as II+III combined. Galea very long, distinctly longer than palpus; galeomere I short, stout; II elongate, hook-like, apically sharp and inward directed, about two times as long as I; galea+palpus distinctly up-curved. Lacinia (Figs 1e, 3d) very short and slender, almost straight, strongly sclerotized, basally fused with stipe. Labium (Figs 1f, 3f) with slightly sclerotized prementum and 2-jointed palpi; prementum subrectangular, distinctly decreasing in width from base to apex; small setal notches present on dorsal surface and sides; ligula very short, dome-like, sub-dorsal; labial palpomere I cylindrical, slightly shorter and wider than II; II digitiform, slightly compressed apically.

Thorax. Tergites (Figs 4a, 5a) scarcely sclerotized, sternum not sclerotized. Pronotum wider than meso- and metanotum, transverse, about two times wider than long. Meso- and metanotum widely transverse, about two and a half times wider than long; longitudinal ecdysial line well marked on pro- and mesonotum, less evident, but present, on metanotum.

Spiracles. Thoracic and abdominal spiracles (Figs 5e, f) annular-uniphorous; mesothoracic spiracles dome-like, anterolateral on mesopleura, more than twice the size of the abdominal spiracle I. Abdominal spiracles rounded, plate-like, not protruding (Fig. 5f), placed dorsolaterally between tergites and epipleurites.

Legs. Legs well developed, 5-jointed (Fig. 4b), forelegs slightly shorter than others, mid and hind legs subequal. Coxa cylindrical, very long, about as long as trochanter and femur combined; trochanter elongate, obliquely truncate and fused apically to femur, about as long as femur and tibia combined; femur about as long as tibia and tarsus combined; tibia very short, cylindrical, slightly shorter than tarsus; tarsus more slender than tibia, conical, tapered from base to apex, with 2 sharp unequal claws (Fig.

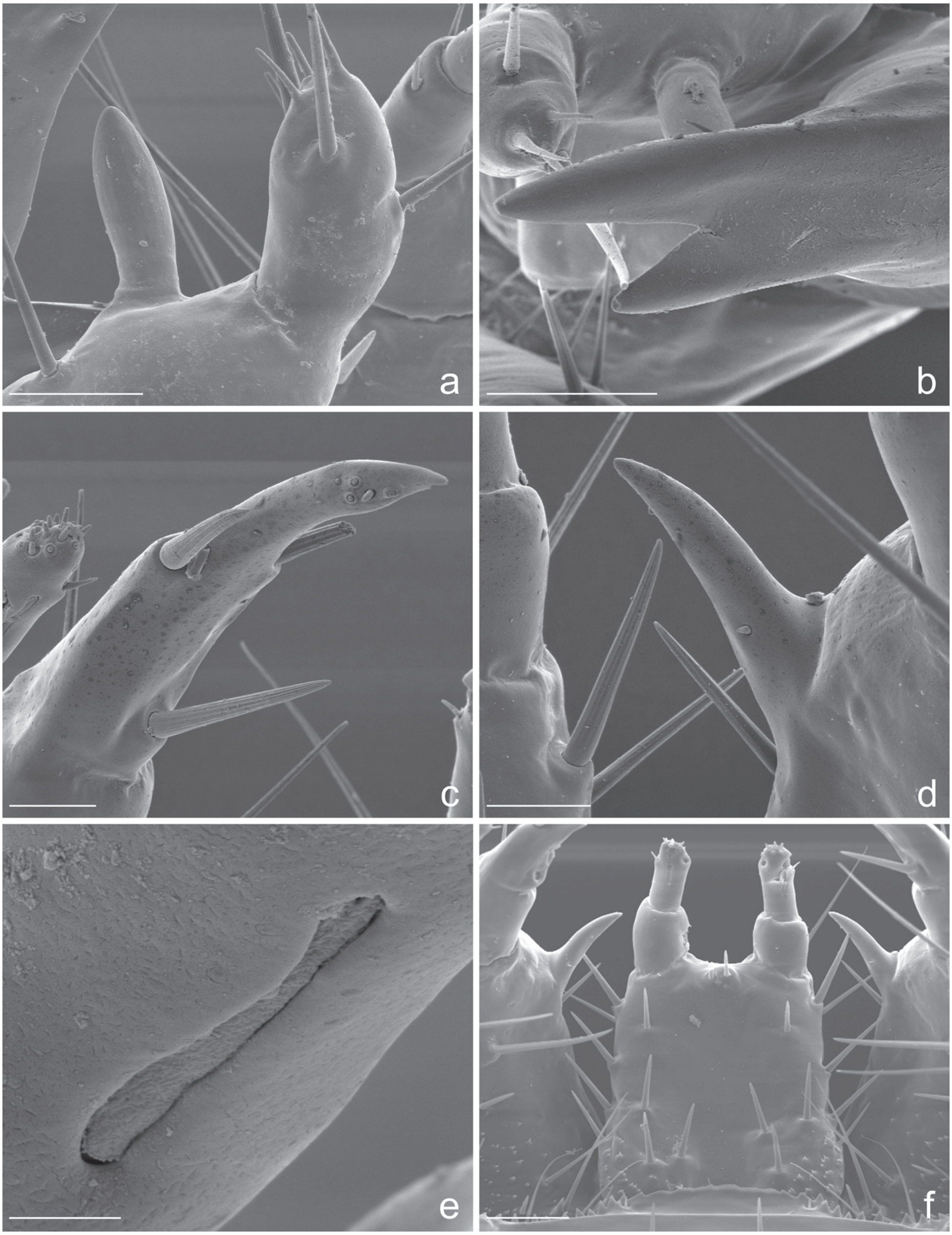

Figure 3. *Eustra chinensis* first instar larva: SEM micrographs of **a** apex of left antenna, dorsal view **b** apex of left mandible, lateral view **c** apex of left galea, dorsal view **d** right lacinia, dorsal view **e** digitiform sensillum of maxillary palpomere IV, lateral view **f** labium, dorsal view. Scale bars: **a** = 20 µm; **b**, **f** = 25 µm; **c**, **d** = 10 µm; **e** = 2 µm.

5b): anterior claw elongate and strong, slightly longer than tarsus, apically curved; posterior claw very small and somewhat obsolescent.

Abdomen. Abdominal segments I-VII (Figs 4c, d) not sclerotized, bellows-like, usually up-curved, keeping the abdominal apex in an elevated position. Abdominal sclerites barely discernable, recognised by reduction of multipointed microsculpture around setae or sensilla S-II; segments progressively wider from I to VIII. Each segment dorsally flattened, with swollen, setiferous pleural and sternal areas. Hypopleurites setiferous, slightly protruding; hypopleurite VI with ventrolateral, elongate digitiform protuberance, tipped by strong spine-like seta. Epipleurites conical, distinctly protruding, gradually more developed from segment I to VIII; epipleurites of segment VIII (Figs 4c-d, 6a, 7d) flattened and enlarged into two sclerotized lateral plates, smaller than the dorsal plates; lateral plates slender, triangular, about two times longer than wide at base; epipleurites of segment IX greatly enlarged and fused with tergum of segment VIII into two rectangular, sclerotized plates (dorsal plates), slightly enlarged from base to apex and widely separated in the middle by a deep V-shaped notch (Figs 4c-d, 6a); lateral plates widely separated from dorsal plates; lateral plates, dorsal plates and urogomphi forming a terminal disk articulated at base by membranes, dorsal and lateral plates move against urogomphi. Urogomphi (Figs 6a, 7a,c) wide, flattened, each composed of 7 pointed lobes: A, B, C, X, E2, E1b, E1a (respectively from the inner to the outer); A much shorter than B; pygidium (Figs 6a, 7a) protruding, medioventrally positioned between the urogomphal insertions.

Eustra chinensis, second and third instar larvae

General morphology very similar to that described above for the first instar, except for: progressive increasing of relative dimensions (see Table 1); presence of secondary setae on antennomere II (2 setae); sensorial appendage much shorter than antennomere IV;

Table 1. Measurements (mm) of three instars (L_1, L_2, L_3) of *Eustra chinensis* and the third instar (L_3) of *Eustra* sp. Taiwan. BL = body length (from tip of mandibles to the apex of terminal disk); HW = cephalic capsule maximum width (at the base of the antennae); HL = cephalic capsule medial length (mesodorsally, from occipital foramen to anterior margin of frontoclypeolabrum); PW = prothorax maximum width; PL = prothorax medial length; TDW = terminal disk maximum width (at the level of lateral plates); DPL = dorsal plates length (from base, near articulation, to the medial apex).

	E. chinensis L_1	*E. chinensis* L_2	*E. chinensis* L_3	*E.* sp. L_3
BL	1.75	2.7	3.02	-
HW	0.39	0.5	0.68	-
HL	0.21	0.28	0.37	-
PW	0.32	0.45	0.65	0.8
PL	0.19	0.28	0.42	0.55
TDW	0.5	0.7	0.98	1.42
DPL	0.22	0.33	0.5	0.62

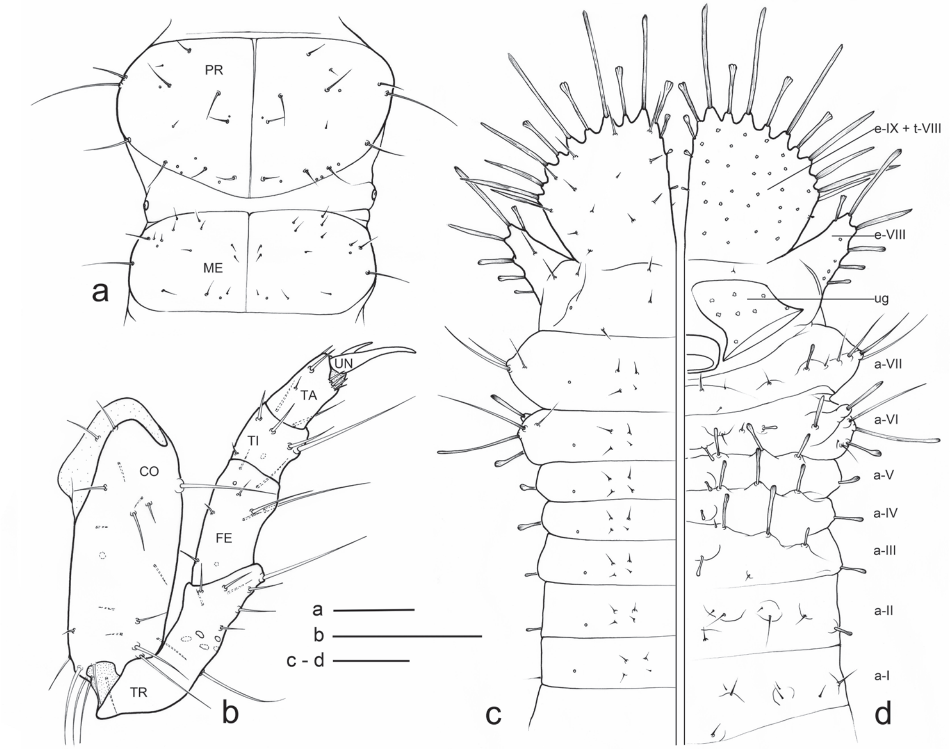

Figure 4. *Eustra chinensis* first instar larva: line drawings of **a** pro- and meso-notum, dorsal view **b** left foreleg, anterior view **c** right side of abdomen, dorsal view **d** right side of abdomen, ventral view (right urogomphus not drawn). a- = abdominal segment; e- = epipleurite; t- = tergum; Scale bars: 0.1 mm.

retinaculum progressively longer and more falcate; stipe with wider and sharp sub-basal protuberance; labial palpomere I wider than II; tibia subequal to tarsus; pronotum about as wide as meso- and metanotum; dorsal plates of terminal disk slightly longer; lobes of urogomphi relatively longer and more slender; lobe E1a slightly longer than E1b.

Eustra sp. Taiwan, third instar larva

Unfortunately, the specimen is damaged and portions of its head and legs are missing. Only basal part of head capsule, basal half of a mandible, thorax, basal part of legs, entire abdomen and terminal disk are intact. However, there is one low-resolution image of the entire specimen, which provides only limited information of some structural details.

General larval structure and most characters of the terminal disk (Fig. 6b) are very similar to those described above, especially as compared with the third instar of *E. chinensis*, except for the following minor differences:

(1) lobe A of urogomphi about as long as B (A much shorter than B in *E. chinensis*); (2) E1a thinner and more elongate than E1b (subequal or only slightly longer to E1b in *E. chinensis*); (3) lobes A very close medially, almost touching (distinctly separated medially in *E. chinensis*).

Discussion

Eustra larvae are highly modified compared with the other known larvae of Ozaenini, and have several unique structures that make their identification easy. These include:

1. Antennae 3-jointed (Figs 1c, 2c). Paussinae larvae generally show 4-jointed antennae, a condition typical for adephagans. The reduction to 3 joints in *Eustra* is clearly due to the fusion of antennomeres II and III.

2. Mandible apically bidentate with sub-basal retinaculum (Figs 1d, 3b). A bidentate mandibular apex is also present in all known myrmecophilous Paussini larvae except *Arthropterus*, but in this tribe the second tooth is thought to be a subapically displaced retinaculum (Di Giulio and Moore 2004). In addition to the bidentate apex (Fig. 3b), a small subtriangular and basally directed retinaculum is present in *Eustra* first instars, and it becomes longer and more falcate in later instars.

3. Ental margin of retinaculum with additional small sub-basal tooth (Fig. 1d). This margin is straight only in *Physea*, while it is more or less sinuate (basal half convex, distal half concave) in all other known ozaenine genera. The presence of a sub-basal tooth on the ental margin in *Eustra* may be an adaptation for piercing and holding their prey.

4. Maxillary palp 3-jointed (Fig.1e). The reduction of the palpomeres from 4 to 3 is a common feature of known Paussini larvae except for *Platyrhopalopsis* and *Arthropterus*. In the genus *Paussus* the reduction is due to the fusion of basal palpomere with the stipe. In *Eustra* the basal palpomere is only partially fused with stipe but still recognizable, and the actual reduction is due to the fusion of palpomeres II+III.

5. Galea extremely long and apically sharp (Figs 1e, 3c). The galea of *Eustra* is two-jointed as is typical of ozaenines but it is highly modified: it is very strong, up-curved, and almost two times longer than the maxillary palp and almost three times longer than the lacinia. The apex is hook-like and unusually sharp, which would provide an effective tool for capturing and holding prey.

6. Strongly asymmetric tarsal claws (Figs 4b, 5b). All Metriini, Mystropomini, and Ozaenini larvae have legs with two tarsal claws of unequal size, the anterior distinctly longer than posterior, while myrmecophilous Paussini larvae have only a single claw (presumably the anterior). In *Eustra* the posterior tarsal claw is extremely small and almost obsolescent.

7. Hypopleurite VI with ventrolateral, elongate digitiform protuberance, tipped by strong spine-like seta (Figs 4d, 5d). This peculiar sensorial structure is unique to the genus *Eustra*.

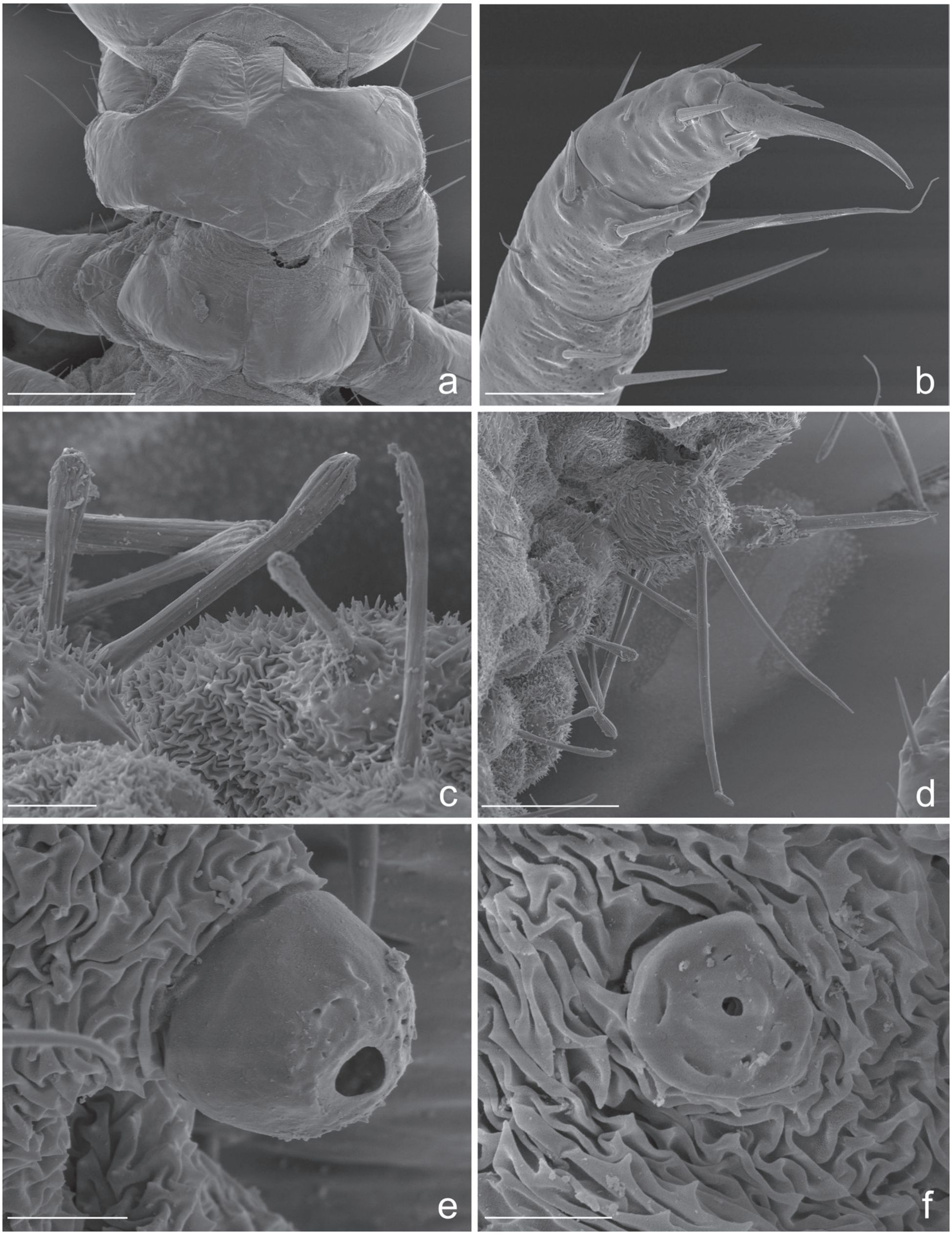

Figure 5. *Eustra chinensis* first instar larva: SEM micrographs of **a** pro- and meso-notum, dorsal view **b** apex of left hind-leg, anterior view **c** abdominal sensilla on left pleurae, dorsal view **d** abdominal sensilla on left pleurae, dorsal view **e** right metathoracic spiracle **f** abdominal spiracle I. Scale bars: **a** = 100 μm; **b** = 30 μm; **c** = 10 μm; **d** = 50 μm; **e** = 5 μm; **f** = 4 μm.

8. Most sternal and pleural setae of the abdomen elongate and clavate at apex (Figs 4c-d, 5c-d). Clavate sensilla have been described in the myrmecophilous genus *Arthropterus* (sensilla S-VIII possibly homolog to S-II, see Di Giulio and Moore 2004), which surround the terminal disk, and are also present on the thorax and cephalic capsule. In *Eustra*, a clavate modification affects most abdominal mechanoreceptors as well as most sensilla of the terminal disk (see below). In particular, the terminal disk has two types of sensilla, often alternate (i.e. dorsal plates): type 1 is very long, stick-like, and pointed at the apex; type 2 is short and clavate at the tip.

9. Lateral plates of terminal disk transverse, subtriangular and pointed at apex (Figs 6a-b, 7d), with straight margins. The lateral plates of the Metriini, Mystropomini

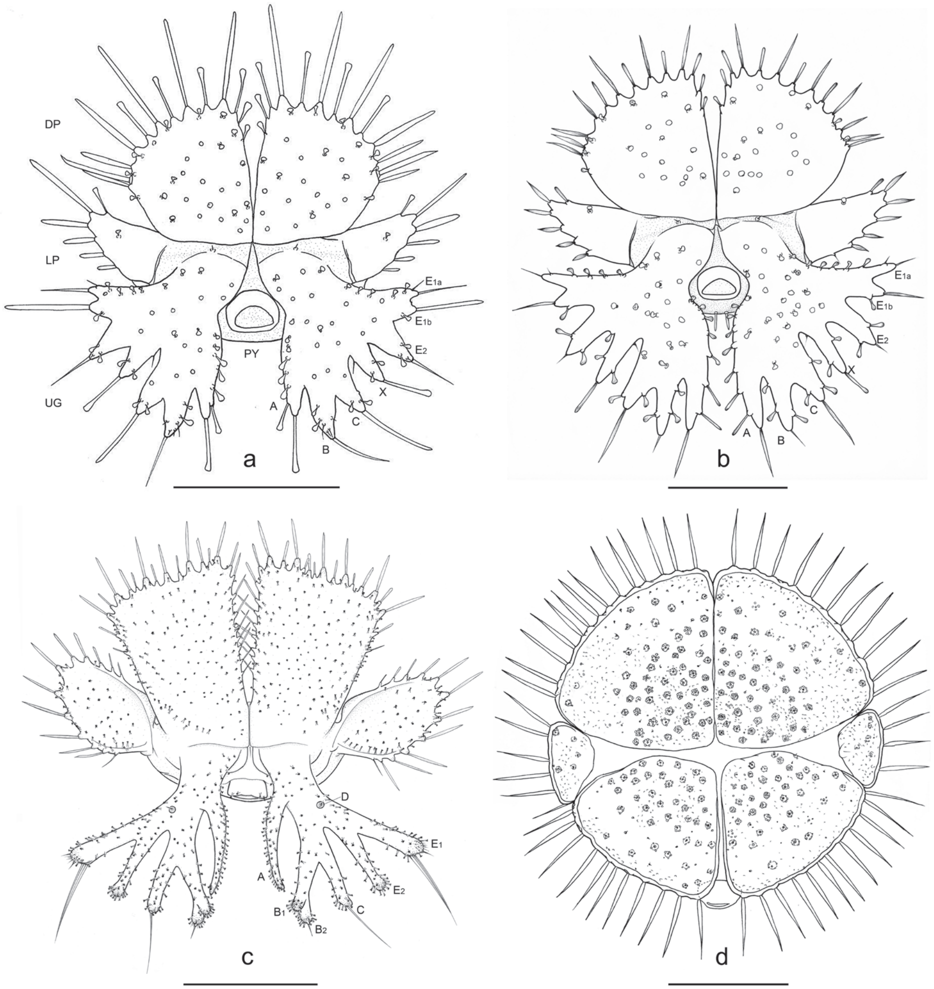

Figure 6. Terminal disks of: **a** *Eustra chinensis* first instar **b** *Eustra* sp. Taiwan third instar **c** *Goniotropis kuntzeni* first instar **d** *Paussus favieri* first instar. DP = dorsal plate; LP = lateral plate; UG = urogomphus; PY = pygidium. Scale bars: a = 0.25 mm; b= 0.5 mm.

and other Ozaenini are wide and broadly rounded. Lateral plates of *Goniotropis* (Ozaenini) (Fig. 6c) are transverse and widely separated from dorsal plates similar to those of *Eustra*.

10. Urogomphi flattened, wider and longer than dorsal plates, composed by 7 short triangular lobes (Figs 6a-b, 7a), acute or bidentate at apex, separated by V-shaped notches of different depths, very shallow as compared to other Ozaenini. The flattening and widening of the urogomphi and the reduction (*Physea*, Ozaenini) or absence (all Paussini, see for example Fig. 6d) of branches is a typical feature of myrmecophilous larvae (Di Giulio et al. 2003; Di Giulio and Moore 2004).

11. Absence of urogomphal lobe D and presence of the additional urogomphal lobe X (Figs 6a-b, 7a). The lobes of urogomphi were coded first in *Metrius* by Bousquet (1986) and his notation was later slightly modified for ozaenines to include the partial or total bipartition of lobes B (B_1+B_2) and E (E_1+E_2) (Vigna Taglianti et al. 1998). This notation works for all described ozaenine larvae except for *Eustra*, which do not have a lobe D, but rather have an additional lobe (here named “lobe X”) located between lobes C and E_2. Lobe X may be interpreted as: (1) a unique lobe (X = F); (2) D-lobe distally displaced to the margin (X = D); or (3) an additional subdivision of lobe E (X = E_3). *Eustra* larvae also have a unique subdivision of E_1 (E_{1a}, E_{1b}).

12. Peculiar inflated sensilla S-I (Figs 7a,c,e) of different lengths present on surface of plates and urogomphi. Inflated sensilla S-I have been described in larvae of *Platyrhopalopsis* (Paussini) and *Physea* (Ozaenini) and have been considered as an adaptation to the myrmecophilous lifestyle (Di Giulio et al. 2003). The sensilla S-I of *Eustra* are very different from the homologous structures of the aforementioned taxa since these are mushroom-shaped, composed of an elongate basal stem, which emerges from a cuticular protuberance, and an apical irregular inflation.

Like in the other ozaenine genera, larvae of *Eustra* live in galleries that they dig in humid soil or rotten wood and close off with their terminal disk, which they use to trap prey. However, the larvae of *Eustra* are so specialized and modified that it is not possible to find clear synapomorphies with larvae of any of the other known ozaenine genera. Some of the peculiar adaptations discussed above are similar to, but not necessary homologous to, characteristics described for the myrmecophilous larvae of Paussini and *Physea* (See Table 2). Since the *Eustra* larva from Taiwan was found inside a nest of *Pachycondyla javana*, it is possible that some of these traits are adaptations to a myrmecophilous lifestyle. However, we think that it is more likely that these minute larvae feed on very small invertebrates like collembolans and *Drosophila*, which first instar ozaenine larvae consistently consume in the lab (Moore and Di Giulio, pers. obs.), than it is that they feed on *Pachycondlya*, which are relatively large-bodied ants. Instead, many of the unusual characters observed in these larvae could facilitate feeding on fast moving prey, including the very long radial mechanoreceptors (sensilla S-II) of the terminal disk which would sense the approach of fast collembolans, and modified mouthparts including the bidentate

Table 2. Characteristics of *Eustra* larvae that are similar to those found in mymecophilous larvae.

Eustra+Physea	galea elongate (but in a completely different way: in *Physea* galeomere I long, II short and truncate at apex; in *Eustra* I short and II very long and sharp)
	lacinia reduced
	prementum elongate and tapered from base to apex
	labral spine wide
	ligula absent
	urogomphal lobes partially fused
	head short and transverse
	frontoclypeolabrale wide and transverse
	coronal suture short
	anterior arms of frontal sutures only slightly sinuate
	stemmata absent
	retinaculum in first instar triangular, inward directed
	sensilla S-I inflated
Eustra+Paussini	mandibles apically bidentate
	number of maxillary palp articles reduced (but in a completely different way, see Discussion)
	second tarsal claw reduced (in Paussini second claw is absent)
	sensilla clavate or inflated (only in *Arthropterus* clavate sensilla S-II, inflated S-I in *Platyrhopalopsis*)
	urogomphal lobes short rather then strongly branched
	urogomphi flat and wide
	antennae short and strongly directed medially
	stemmata absent
	sensorial appendage elongate
	head shortened and distinctly transverse

mandibular apex, second tooth of retinaculum, and hook-like galea which would help the larva hold onto motile prey. Other characters, such as the flattening and widening of the urogomphi, could be related to the miniaturization of the larval body. In the future, we hope to discover the larvae of the genus *Dhanya,* and compare its morphological structures with *Eustra* since they are hypothesized to be sister genera (Jeannel 1946; Stork 1985; Deuve 2001), as well as larvae of the species formerly classified in the genus *Ozaenaphenops* to search for support of its synonymy with *Eustra* (Deuve 2001).

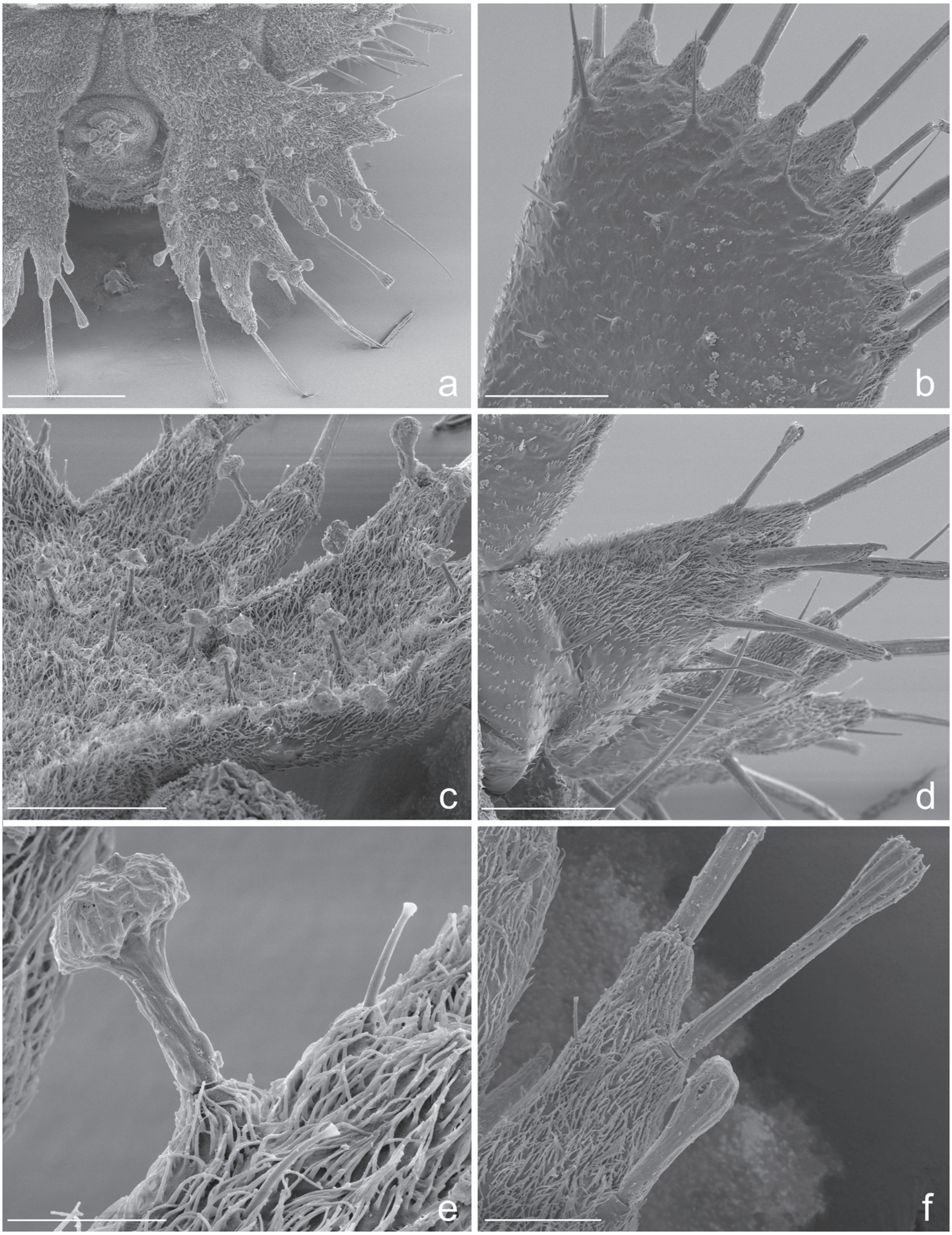

Figure 7. *Eustra chinensis* first instar larva: SEM micrographs of **a** right urogomphus, dorsal view **b** left dorsal plate, dorsal view **c** right urogomphus, left dorso-lateral view **d** left lateral plate, dorsal view **e** sensillum S-I on X lobe, lateral view **f** right urogomphus, lobe A, dorso-lateral view. Scale bars: **a** = 100 µm; **b**, **c**, **d** = 50 µm; **e** = 10 µm; **f** = 20 µm.

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