

The groundwater-dwelling fauna of South East Asia

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ABSTRACT

Groundwater fauna consists of organisms that are adapted to live their whole life-time in different types of groundwater (=aquifers): with fissured (karstic) and porous (alluvium) types as the most common. About 3800 species of obligate groundwater species (stygobionts) have been recorded worldwide and 2000 of them from groundwater in Europe. Before 1970, 19 species of stygobionts were known from Southeast Asia. After 1980, the number of stygobionts from this region started to increase, and, at present, 122 stygobionts are known here. Most of them are crustaceans, with the Copepoda, Isopoda, Amphipoda and Decapoda as the most abundant groups. Intensification of research on groundwater fauna can considerably increase the total number of stygobionts known from the region, which could rise up to several times the current tally if the intensity of research was comparable with that in Europe.

Key words: Caves, groundwater fauna, karst, Southeast Asia, stygobionts.

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INTRODUCTION

More than half of the stygobionts (*i.e.* obligate groundwater dwellers) reported globally are known from Europe. In total, there are about 3800 known stygobionts worldwide and about 2000 taxa are reported from groundwater in Europe (Gibert and Culver, 2009). This is the result of long-term research in fissured (*i.e.* karstic) and porous (*i.e.* alluvium, interstitial) aquifers in Europe.

The first information related to stygobionts arose from caves and karstic springs, because animals there are relatively larger, more noticeable and easier to collect than animals in porous aquifers. Records were made sporadically as a result of occasional visits to caves or investigation of wells and were focussed mainly on larger body-sized groups like Isopoda, Amphipoda, Decapoda and Pisces. Some rare records on *micro-crustacea* from caves or wells have been existing for a long time as well [Tab. 1; after Botosaneanu (1986)]. Among the first records of groundwater fauna were those of Copepoda from the drinking water system of St. Petersburg from 1866 (although specimens recorded there were actually stygophiles) and of Bathynellaceae from a similar environment in Prague (in 1882) (Botosaneanu, 1986; Camacho, 1992).

Among the first described stygobionts (some of them were actually stygophiles) were amphibians (*Proteus anguinus* Laurenti, 1768), fish [*Monopterus albus* (Zuiw, 1793)] and amphipods [*Gammarus minus* (Say, 1818), *Niphargus puteanus* (C.L. Koch, 1836)], followed by

crabs and shrimps [*Orconectes pellucidus* (Tellkampf, 1844), *Troglocaris anophthalmus* (Kollar, 1848)]. In contrast, stygobiotic Calanoida, also present in Southeast (SE) Asia, have been found just recently [*Microdiaptomus cokeri* (Osorio Tafall, 1942)] (Tab. 1). The main reason for their late discovery, is the generally rather low numbers of freshwater stygobiotic Calanoida (Brancelj and Dumont, 2007).

The intensity of research related to groundwater fauna increased after the First World War and since then it has been increasing, not only in Europe but worldwide. Most recently, among the most intensive projects on groundwater and its fauna, which included both types of aquifers, was the project Protocol for the Assessment and Conservation of Aquatic Life in the Subsurface (PASCALIS; available from: <http://pascalis-project.com/>) that was conducted in Europe during the period 2002-2005 (Deharveng *et al.*, 2009; Stoch and Galassi, 2010). The project revealed that even in areas with intensive and continuous research of groundwater fauna there was still a big potential for discovering new species. In six European regions with a total area of 11,777 km², 217 species were known before project PASCALIS, and after the project the number increased to 379, with 109 new species for those six regions, including some that were new to science (Deharveng *et al.*, 2009; Dole-Olivier *et al.*, 2009). For example, intensive and systematic sampling of porous aquifers along the rivers, which were included in the PASCALIS project, resulted in a discovery of rich population of two

Tab. 1. List of the first three stygobiotic species of each higher taxonomic group described and present elsewhere in the world. Representatives of higher taxonomic groups are also present in Southeast Asia but with different species [data from Botosaneanu (1986)].

Turbellaria			
1	<i>Phagocata vitta</i> (Duges, 1830) Europe, the Alps, Balkan	<i>Dendrocoelum nausicae</i> Schmidt, 1861 South Europe and Anatolia	<i>Phagocata olivacea</i> (Schmidt, 1862) Southeast Adriatic coast
Nematoda			
2	<i>Pseudorhabdolaimus limnophilus</i> Soos, 1937 Hungary, Austria	<i>Thalassoalamus aquaedulcis</i> Schneider, 1940 Slovenia	<i>Criconema minor</i> (Scheider, 1940) Slovenia
Oligochaeta			
3	<i>Trichodrilus pragensis</i> Vejdovsky, 1875 Czech lands	<i>Trichodrilus intermedius</i> Fauvel, 1903 France	<i>Trichodrilus cantabrigensis</i> Beddard, 1908 United Kingdom
Ostracoda			
4	<i>Pseudocandona eremita</i> (Vejdovsky, 1880) Central and South Europe	<i>Sphaeromicola topsenti</i> Paris, 1916 France	<i>Pseudocandona zschokkei</i> (Wolf, 1919) West and Central Europe
Copepoda			
<i>Calanoida</i>			
5	<i>Microdiaptomus cokeri</i> Osorio Tafall, 1942 Mexico	<i>Speodiaptomus birsteini</i> Borutzky, 1962 Krim peninsula (Ukraine)	<i>Ridgewayia marki</i> (Esterly, 1911) - anchialine, Bermuda islands
<i>Cyclopoida</i>			
6	<i>Diacyclops languidoides</i> (Lilljeborg, 1901) Europe	<i>Acanthocyclops venustus</i> (Norman and Scott, 1906) Europe	<i>Eucyclops terras</i> (Graeter, 1907) Switzerland
<i>Harpacticoida</i>			
7	<i>Parastenocaris fontinalis</i> Schnitter and Chappuis, 1915 Europe	<i>Bryocamptus pyrenaeicus</i> (Chappuis, 1923) France, Slovenia	<i>Nitocrella hirta</i> Chappuis, 1923 Europe
Syncarida			
8	<i>Bathynella natans</i> Vejdovsky, 1882 Europe	<i>Anaspides tasmaniae</i> (Thomson, 1893) Tasmania (Australia)	<i>Bathynella chappuisi</i> Delachaux, 1920 Europe
Isopoda			
<i>Cirolanidae</i>			
9	<i>Cirolanides texensis</i> Benedict, 1896 Texas (USA)	<i>Spahaeromides raymondi</i> Dollfus, 1897 France	<i>Faucheria faucherii</i> (Dolphus and Virè, 1900) France
<i>Sphaeromatidae</i>			
10	<i>Monolistra caeca</i> Gerstaeker, 1856 Slovenia	<i>Caecosphaeroma virei</i> Dollfus, 1896 France	<i>Caecosphaeroma burgundum</i> Dollfus, 1896 France
<i>Anthuridea</i>			
11	<i>Cruregens fontanus</i> Chilton, 1881 New Zealand	<i>Cyanthura curassavica</i> Stork, 1940 Central America	<i>Cyanthura milloti</i> Chappuis, Delamare Deboutteville and Paulian, 1956 Reunion island
<i>Asellota</i>			
12	<i>Caecidotea stygia</i> Packard, 1871 Central part of USA	<i>Caecidotea nickajackensis</i> Packard, 1881 Tennessee (USA)	<i>Asellus hilgendorfi</i> Bovalius, 1886 Japan
<i>Microcerberidae</i>			
13	<i>Microcerberus stygius</i> Karaman, 1933 Macedonia	<i>Microcerberus remanei</i> Chappuis and Delamare, 1952 Mediterranean area	<i>Microcerberus delamarei</i> Remane and Siewing, 1953 Brazil
<i>Phreatoicidea</i>			
14	<i>Phreatoicus typicus</i> Chilton, 1882 New Zealand	<i>Neophreatoicus assimilis</i> Chilton, 1884 New Zealand	<i>Phreatoicoides gracilis</i> Sayce, 1900 Australia

To be continued on next page.

Tab. 1. Continued from previous page.

Amphipoda			
<i>Gammaridae</i>			
15	<i>Gammarus minus</i> Say, 1818 Central part of USA	<i>Rhipidogammarus rhipidophorus</i> (Catta, 1878) Mediterranean area	<i>Sarathrogammarus guernei</i> (Chevreux, 1889) Azores (Portugal)
<i>Melitidae</i>			
16	<i>Eriopis elongata</i> (Bruzelius, 1859) Europe, USA	<i>Eriopisella sechellensis</i> (Chevreux, 1901) Seychelles	<i>Pseudoniphargus africanus</i> Chevereux, 1901 Algeria
<i>Niphargidae</i>			
17	<i>Niphargus puteanus</i> (C.L. Koch, 1836) Germany, Switzerland	<i>Niphargus stygius</i> (Schiödte, 1847) Slovenia	<i>Niphargus longicaudatus</i> A. Costa, 1851 Italy
<i>Crangonyctidae</i>			
18	<i>Crangonyx subterraneus</i> Bate, 1859 West and Central Europe	<i>Stygobromus tenuis</i> (Smith, 1874) East coast of USA	<i>Batrurus mucronatus</i> (Forbes, 1876) Central part of USA
Thermosbaenacea			
19	<i>Thermosbaena mirabilis</i> Monod, 1924 Tunisia	<i>Monodella stygicola</i> Ruffo, 1949 Italy	<i>Monodella argentaria</i> Stella, 1951 Italy
Decapoda			
<i>Natantia</i>			
20	<i>Troglocaris anophthalmus</i> (Kollar, 1848) Slovenia, Italy	<i>Barbouria cubensis</i> (Von Martens, 1872) Cuba	<i>Caridina japonica</i> De Man, 1892 Japan
<i>Reptantia</i>			
21	<i>Orconeces pellucidus</i> (Tellkampf, 1844) Tennessee (USA)	<i>Orconeces inermis</i> Cope, 1872 Kentucky, Indiana (USA)	<i>Cambarus hamulatus</i> (Cope, 1881) Alabama, Tennessee (USA)
<i>Brachyura</i>			
22	<i>Thelphusula bidiens</i> (Lanchester, 1900) Sarawak, Borneo	<i>Sesarmoides jacobsoni</i> (Ihle, 1912) Central Java, Indonesia	<i>Sesarmoides verleyi</i> (Rathbun, 1914) Jamaica
Acarina			
<i>Hydrachnida</i>			
23	<i>Wandesia thori</i> (Scheethel, 1912) Europe	<i>Frontipodopsis staheli</i> Walter, 1919 Central and South America	<i>Sczizobates disjunctus</i> (Walter, 1925) Argentina
Coleoptera			
24	<i>Siettitia balsetensis</i> Abille de Perrin, 1904 France	<i>Siettitia avenionensis</i> Guignot, 1925 France	<i>Uvarus chappuisi</i> (Peschet, 1932) Burkina Faso
Pisces			
25	<i>Taeniooides anguillaris</i> (Linnaeus, 1758) China	<i>Monopterus albus</i> (Zuiwei, 1793) Myanmar, China, Japan	<i>Trypauchen vagina</i> (Bloch and Schneider, 1801) Taiwan, China

species of stygophilic groundwater dwelling cladocerans. In the past, both species were considered to be very rare, but the many specimens collected during the project enabled a new genus – *Phreatalona*, to be established (Van Damme *et al.*, 2008).

Other parts of the world remained rather *cold spots* for a long time. Until 1964, information on relatively rich

troglobiotic/stygobiotic fauna existed only for Europe and the SE USA. Other parts of the world, including SE Asia, remained very poorly known, even three decades later (Holsinger, 1993). Actually, most of the information on cave-dwelling fauna from SE Asia was limited to terrestrial species (Deharveng, 2004). Among stygobiotic fauna, at least one representative from each main group

of stygobionts so far recorded in SE Asia had already been known from elsewhere before the beginning of the 20th century (Tab. 1). This is an additional indication that stygobiotic fauna in SE Asia was not adequately sampled since relatively recently, *i.e.* after the 1970s.

More recent inventories revealed that about 160 stygobiotic taxa are known from SE Asia and the Indian sub-continent combined (Gibert and Culver, 2009). From the Indian sub-continent, about 50 stygobionts are known; there, several new stygobionts – especially among the micro-crustaceans (Copepoda and Syncarida) – were recently found to live in porous aquifers (Ranga Reddy and Defaye, 2008; Ranga Reddy *et al.*, 2008; Ranga Reddy and Schminke, 2009).

In the present paper a more detailed analysis of stygobiotic fauna in SE Asia is presented, with special emphasis on the most recent investigation of epikarst in Thailand and Vietnam.

METHODS

Southeast Asia includes the countries of Cambodia, Laos, Burma (Myanmar), Thailand, Vietnam and peninsular Malaysia. It also includes the maritime areas of SE Asia: Brunei, East Malaysia, East Timor, Indonesia, the Philippines and Singapore (Wikipedia, 2013). Total land area is about 4,300,000 km², 408,000 km² (9.7%) of which is karstic (Day and Urich, 2000; Tab. 2). Apart from the karstic areas, there are also vast alluvial areas, with an array of potential habitats for stygobiotic organisms (Gibert *et al.*, 1990).

Data on stygobiotic fauna from the countries of SE Asia was collected from various literature sources. For the period up to 1986, the source was *Stygofauna Mundi* (Botsaneanu, 1986), where all relevant literature on groundwater fauna worldwide is presented till 1986. For the period between 1986 and 2001 the source was *Encyclopaedia*

Biospeleologica (Juberthie and Decu, 2001). After 2001, individual papers on fauna from SE Asia were used.

To present the intensity of research on stygofauna in SE Asia, a cumulative curve over time was constructed by adding each record of a new stygobiotic species in the region to the previous, already recorded taxa.

RESULTS

Historical overview and present status of stygobionts in Southeast Asia

At the beginning of the 20th century only six stygobionts were known from SE Asia; this increased to 20 species in 1970 and reached 22 species in 1986, when the first list of global and regional stygobiotic fauna was compiled (Tab. 3; Botsaneanu, 1986). In the period between 1986 and 2001 the number of newly recorded species increased by 57 species (Juberthie and Decu, 2001) and in 2012 reached a total number of 122 species included in 74 genera (Fig. 1). In this number are also species from anchialine caves and some species which probably belong to the stygophiles. Most of the newly recorded species were also new to science and thus described in adequate taxonomic papers.

The highest number of stygobionts so far recorded is from Thailand (36 species) and the Philippines (35 species), followed by Indonesia and Malaysia (20 and 19 species, respectively), Vietnam (9 species), Cambodia (3 species), Laos (2 species) and Myanmar (1 species) (Tabs. 3 and 4).

Most of the species are recorded from a single location or, less frequently, from several in close proximity to each other (usually several kilometres). So far, only three species from SE Asia are known from more than one country (*Attheyella vietnamica* Borutzky, 1967: Vietnam and Thailand; *Theosbaena cambodjiana* Cals and Boutin, 1985: Cambodia and Thailand; *Parhippolyte uveae* Borradaile, 1899: Indonesia and Philippines).

Tab. 2. Extent of karstic area per country in Southeast Asia [after Day and Urich (2000)].

Country	Country area (km ²)	Karstic area (km ²)	(%)
Cambodia	181,035	20,000	11.0
Indonesia	1,904,569	145,000	7.6
Laos	236,800	30,000	12.7
Malaysia	131,598	18,000	13.7
Myanmar	676,578	80,000	11.8
Philippines	300,000	35,000	11.7
Thailand	513,120	20,000	3.9
Vietnam	331,689	60,000	18.1
Total	4,275,389	408,000	9.7

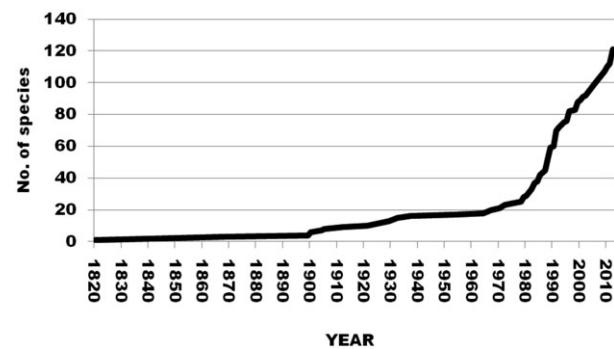


Fig. 1. Cumulative number of stygobiotic taxa recorded in Southeast Asia from 1820 to 2012.

Tab. 3. List of stygobiotic taxa for Southeast Asia, locations of records and habitats.

Taxa	Cambodia	Indonesia	Laos	Myanmar	Philippines	Thailand	Vietnam	Habitat	Location
Turbellaria (4 taxa)									
<i>Dugesia batuensis</i> Ball, 1970	x							Cave	Batu cave near Kuala Lumpur, Gombak district
<i>Dugesia deharvengi</i> Kawakatsu and Mitchell, 1989		x						Cave	Tham Kubio cave, Chum Phae district, Khon Kaen province
<i>Dugesia leclerci</i> Kawakatsu and Mitchell, 1995	x							Cave	Tham Phulu cave, Muang district, Phang Nga province
<i>Micellaia sarawakensis</i> Kawakatsu and Chapman, 1983	x							Cave	Gua Tanette cave, Maros island, Sulawesi
<i>Micellaia sarawakensis</i> Kawakatsu and Chapman, 1983		x						Cave	Waier Polo cave, Gunung Mulu National Park, Sarawak, Borneo
Nematoda (1 taxon)									
<i>Dorylaimus seligerensis</i> De Man, ?	x							Cave	Batu caves near Kuala Lumpur, Gombak district
Oligochaeta (1 taxon)									
<i>Haplotaxis glandularis</i> Yamaguchi, 1953					x			Cave	Tham Kubio cave, Chum Phae district, Khon Kaen province
Ostracoda (2 taxa)									
<i>Baetocypris paradoxa</i> Victor and Fernando, 1980	x							Cave	Batu caves near Kuala Lumpur, Gombak district
<i>Candonopsis pectalis</i> Klie, 1932	x							Spring	Well, Begor island
Copepoda (22 taxa)									
<i>Asiacaris dispar</i> Cottarelli, Bruno and Berera, 2010					x			Hyporheic	Than Sadet river, Pha-ngan island, Surat Thani province
(Cottarelli <i>et al.</i> , 2010)					x	x		Cave	Cave in North Vietnam, Lac Thuy district, Hoa Bin province; Tham Bot Wangna cave, Noen Maprang district, Phitsanulok province
<i>Aththeyella (Canthosella) vietnamica</i> Borutzky, 1967					x			Anchialine cave	San Vicent cave, San Vicente
<i>Boholina crasicephalata</i> Fosshagen, 1989	x				x			Anchialine cave	San Vicent cave, San Vicente
<i>Boholina purgata</i> Fosshagen, 1989	x				x			Cave	Tham Nam Phar Ngam cave, Mae Wa National Park, Mae Phrik district, Lampang province
<i>Bryocyclops maewaensis</i> Watirooram, Branceij and Sanoamuang, 2012					x			Cave	Pauh Cave, Buktinggi; Vijer cave near botanic garden; several caves in Kanchanaburi province
<i>Elaphoidella bidens decorata</i> (Sars, 1904)	x				x			Cave	Tham Phar Ngam cave, Jaesom National Park, Wang Nuea district, Lampang province
<i>Elaphoidella jaesomenis</i> Watirooram, Branceij and Sanoamuang, 2013	x				x			Well	Wells on Phuket island, Phuket province
<i>Elaphoidella margaritae</i> Pesce and Apostolov, 1985					x			Cave	Tham Yai Nam Nao cave, Nam Nao National Park, Nam Nao district, Phetchabun province
(Pesce and Apostolov, 1985)					x			Cave	Tham Khun cave, Noen Maprang district, Phitsanulok province
<i>Elaphoidella thailadensis</i> Watirooram, Branceij and Sanoamuang, 2013					x			Cave	Cave in North Vietnam, Lac Thuy district, Hoa Bin province
<i>Elaphoidella vietnamica</i> Borutzky 1967	x				x			Interstitial	Wat Yang Kao temple, Sangkhlaburi district, Kanchanaburi province
<i>Epactophanes philippinus</i> Bruno and Cottarelli, 1999					x			Spring	Cave in North Vietnam, Lac Thuy district, Hoa Bin province
(Bruno and Cottarelli, 1999)					x			Cave	Kao Sawan Badan cave, Sangkhlaburi district, Kanchanaburi province
<i>Fierscyclops solaris</i> Boonyanusith, Branceij and Sanoamuang, 2013					x				To be continued on next page.
<i>Fierscyclops tanasviensis</i> Boonyanusith, Branceij and Sanoamuang, 2013					x				

Tab. 3. Continued from previous page.

Taxa	Cambodia	Indonesia	Laos	Malaysia	Myanmar	Philippines	Thailand	Vietnam	Habitat	Location
<i>Hadadiaptomus dumontii</i> Brancelj, 2005				x		x	Cave	Dang Water cave, Cuc Phuong National Park, Ha Noi		
<i>Halicyclops thermophilus</i> Kiefer, 1929	x					x	Therm. spring	Salt thermal spring, Kurijan, Java		
<i>Microarthridion thamni</i> Tran and Chang, 2012				x		x	Anchialine cave	Cave, Ninh Binh province		
<i>Nitocra vietnamensis</i> Tran and Chang, 2012						x	Anchialine cave	Cave, Ninh Binh province		
<i>Parastenocaris arganoi</i> Cottarelli and Mura, 1982	x					x	Cave	Batu caves near Kuala Lumpur, Gombak district		
<i>Parastenocaris mangians</i> Bruno and Cottarelli, 1999				x		x	Interstitial	Phreatic near Talipanan village, Mindoro island		
(Bruno and Cottarelli, 1999)										
<i>Parastenocaris distincta</i> Cottarelli, Bruno and Berera, 2006 (Cottarelli et al., 2006)				x		x	Interstitial	Phreatic, Mindoro island		
<i>Phyllognathopus hassoti</i> Rouch, 1972				x		x	Interstitial	Shore of Lake Wisdom, New Guinea		
Syncarida (5 taxa)										
<i>Bauabathynella malaya</i> (Sars, 1929)	x				x	x	Cave	Batu caves near Kuala Lumpur, Gombak district		
<i>Paraebathynella vietnamensis</i> Camacho, 2005 (Camacho, 2005)				x		x	Cave	Hang Trinh Nu cave, Bo Hon island		
<i>Sabahbathynella wongi</i> Schminke, 1988										
<i>Siambathynella taorsriae</i> Camacho, Wairogram and Brancelj, 2011					x	x	Interstitial	Sungai Masalong river, Sabah, Borneo		
<i>Sketinella tronefjii</i> Camacho, 2005 (Camacho, 2005)					x	x	Cave	Tham Yai Nam Nao cave, Nam Nao National Park, Nam Nao district, Phetchabun province		
					x	x	Anchialine cave	Cave, Rom island		
Isopoda (21 taxa)										
<i>Amnia fastis</i> (Bowman and Iliffe, 1991)					x	x	Cave	Tham Rusi cave, Muang district, Phang Nga province		
<i>Anopsilana conditionaria</i> Bruce and Iliffe, 1992 (Bruce and Iliffe, 1992)					x	x	Anchialine cave	Cave on islet north of Koron island		
<i>Anopsilana lingua</i> Bowman and Iliffe, 1987					x	x	Cave	Cave, Palau islands, Republic of Palau		
<i>Cyathura (Sygocyathura) chapmani</i> Andreev, 1982					x	x	Cave	Gua Air Jernih cave, Gunung Mulu National Park; Borneo Caesar's cave, well, Battian, Bohol island		
<i>Cyathura (Sygocyathura) filipinica</i> Botosaneanu and Sket, 1999 (Botosaneanu and Sket, 1999)					x	x	Interstitial	Interstitial 1.3 m deep, Bambu river, Papua New Guinea, Lae Morobe province		
<i>Cyathura (Sygocyathura) papuiae</i> Weagle, Coleman and Hosse, 1987 (Weagle et al., 1987)					x	x	Cave	Tham Phanthurat cave in Khao Sok National Park, Phanom district, Surat Thani province		
<i>Stenasellus bedosae</i> Magniez, 1991					x	x	Cave	Caves in Batammbang province		
<i>Stenasellus boutini</i> Magniez, 1991					x	x	Spring	Spring, Phuket island, Phuket province		
<i>Stenasellus brignolii</i> Pesse and Argano, 1981					x	x	Cave	Cave near Kampung Trach district, Kampot province,		
<i>Stenasellus cambodianus</i> Boutin and Magniez, 1985	x				x	x	Cave	Snake cave, Water Polo cave, New High Level cave, Sarawak, Borneo		
<i>Stenasellus chapmani</i> Magniez, 1982					x	x	Cave	Bat Quarry cave, Aceh Besar, Sumatra		
<i>Stenasellus covillae</i> Magniez, 1987				x		x	Cave	Tham Keo cave near Nlong Bua Daeng, Phakdi Chumphon district, Chaiyaphum province		
<i>Stenasellus deharvengi</i> Magniez, 1991					x	x	Cave	Ngala Surat cave, Ngala Pelyangan cave, Sumatra		
<i>Stenasellus foresti</i> Magniez, 2002				x		x				To be continued on next page.

Tab. 3. Continued from previous page.

Taxa	Cambodia	Indonesia	Laos	Malaysia	Myanmar	Philippines	Thailand	Vietnam	Habitat	Location
<i>Stenasellus javanicus</i> Magniez and Rahmadi, 2006 (Magniez and Rahmadi, 2006)	x								Cave	Cikaray cave, Leuwili Kares island
<i>Stenasellus mongnatei</i> Magniez and Pantivong, 2005 (Magniez and Pantivong, 2005)				x					Cave	Tham Nam cave, Kaeng Khoi district, Saraburi province
<i>Stenasellus monodi</i> Magniez, 2000	x								Cave	Ngalaub Lagung cave, Sumatra
<i>Stenasellus rigali</i> Magniez, 1991			x						Cave	Tham Kubio cave, Chum Phae district, Khon Kaen province
<i>Stenasellus stocki</i> Magniez, 2001	x								Cave	Ngalaub Indah cave, Sumatra
<i>Stenasellus strinatti</i> Magniez, 1991	x								Cave	Ngalaub Baso cave, Ngalaub Kamang cave, Sumatra
<i>Thalandoniscus annae</i> Dalens, 1989			x						Cave	Springs near the Tham Tapan cave, Muang district, Phang Nga province
<hr/>										
Amphipoda (13 taxa)										
<i>Aequigidiella aquilifera</i> Botosaneanu and Stock, 1989			x						Cave	Tham Phulu cave, Muang district, Phang Nga province; Tham Keao cave, Phakdi Chumphon district, Chaiyaphum province
<i>Bogidiella daccordii</i> Ruffo, 1994				x					Interstitial	Phreatic on Palawan island, St. Paul subterranean river Nat Park, Western Visayas
<i>Bogidiella deharvengi</i> Stock and Botosaneanu, 1988			x						Cave	Batu Lubang cave, Halmashera island
<i>Bogidiella (Medigidella) sarawacensis</i> Stock, 1983			x		x				Cave	Niah Great cave, Batu Niah National Park, Sarawak, Borneo; Deer cave, Gunung Mulu National Park, Sarawak, Borneo
<i>Bogidiella thai</i> Botosaneanu and Noteboom, 1988				x					Cave	Tham Poung Chang cave, Muang district, Phang Nga province
<i>Bollegidia sootai</i> (Coineau and Rao, 1972)				x					Interstitial	Interstitial, Sabang beach, eastern Mindoro, Palawan islands
<i>Cottarellia minima</i> Ruffo, 1994				x					Interstitial	Interstitial, Sabang beach, eastern Mindoro, Palawan islands
<i>Eriopsis philippensis</i> (Chilton, 1921)				x					Well	Well near Los Baños, southern shore of Laguna de Bay, Luzon Island
<i>Flagiitopsis fluviatilis</i> (Stock, 1991)					x				Interstitial	Pagsanjan falls, Laguna province, Luzon island
<i>Paraniphargus rutherfordi</i> Schellenberg, 1931					x				Cave	Batu Lubang cave, Halmahera, east Java
<i>Psammogammarus florianus</i> Stock, 1991					x				Interstitial	Gravel bar near Pagsanjan falls, Laguna
<i>Seborgia vietnamica</i> Jaume, Sket and Boxshall, 2009 (Jaume et al., 2009)					x				Cave	Cave Dong Duc Tie, Dao Van Gio island
<i>Tegano barnardi</i> Sawicki and Holsinger, 2005	x								Cave	Airport well cave, Peleliu island
<hr/>										
Thermosbaenace (2 taxa)										
<i>Thecosbaena cambodiana</i> Cals and Boutin, 1985	x				x				Cave	Cave near Kampong Trach district, Kompong Trach province
<i>Thecosbaena sp.</i>			x						Cave	Tham Kubio cave, Chum Phae district, Khon Kaen province
<hr/>										
Decapoda (Natantia, Reptantia and Brachyura) (33 taxa)										
<i>Adelana chapmani</i> (Holthuis, 1979)	x								Cave	Niah Great cave, near Miri, Borneo
<i>Archinoeithopussa rhadamanthys</i> (Ng and Goh, 1978)	x								Cave	Simud Putch cave, Sabah, Borneo
<i>Archinoeithopussa covernicola</i> Taedea, 1983			x						Cave	Quinanon-an cave, Arneoneira, Bohol, island

To be continued on next page.

Tab. 3. Continued from previous page.

Taxa		Country	Cambodia	Indonesia	Laos	Malaysia	Myanmar	Philippines	Thailand	Vietnam	Habitat	Location
<i>Archiploethelphusa longipes</i> Bals., 1937			x							x	Cave	Bautakay cave, Aimonau, Quezon province, Luzon island
<i>Cancracaea xenomorpha</i> Ng, 1991 (Ng, 1991)	x									x	Cave	Gua Tanette cave, Lubang Batu Neraka cave, cave in Maros, Maros, Sulawesi
<i>Cerberusa coeca</i> Holthuis, 1979	x									x	Cave	Deer cave, Green cave, Clearwater cave, Gunung Mulu National Park, Sarawak, Borneo
<i>Cerberusa tipula</i> Holthuis, 1979	x									x	Cave	Clearwater cave, cave of Winds, Wonder cave, Gunung Api masiff, Gunung Mulu National Park, Sarawak, Borneo
<i>Edoneus atheistus</i> Holthuis, 1978						x				x	Cave	Subterranean river near Santiago, Isabela province, Luzon island; cave near Sitio Disluad, Aglipay Quirino province, Luzon island
<i>Edoneus ervini</i> Cai and Husana, 2009 (Cai and Husana, 2009)					x					x	Cave	Bantakay cave, Luzon island
<i>Edoneus marulas</i> Cai and Husana, 2009 (Cai and Husana, 2009)					x					x	Cave	Marulas caves, Luzon island
<i>Edoneus skeri</i> Cai and Husana, 2009 (Cai and Husana, 2009)					x					x	Cave	Bantakay cave, Luzon island
<i>Erebusa callobates</i> Yeo and Ng, 1999					x					x	Cave	Than Tê cave, Thakhek district, Khammouane province
<i>Karsztarma philippinum</i> Husana, Naruse and Kase, 2010 (Husana et al., 2010)					x					x	Anchialine Bat cave, Boracay island; Tagbaobo cave, Samal island cave	Anchialine Bat cave, Boracay island; Tagbaobo cave, Samal island
<i>Macrobrachium poentz</i> Holthuis, 1984	x									x	Cave	Several caves, probably only in Gunung Sewu Karst
<i>Nemoron nomas</i> Ng, 1996						x				x	Cave	Cave in Phong Nha, Hang Toi, Quang Binh province
<i>Parhippolyte inaeae</i> Borradaile, 1899					x					x	Cave	Tiniguanban cave, Gimaras, Tinigualban island; Holmahera, Maluccas
<i>Phaibulamon stiliipes</i> Ng, 1992					x					x	Cave	Tham Nam Phra Khan cave, Sangkhlaburi district, Kanchanaburi province
<i>Phricothelphusa deharvengi</i> Ng, 1988					x					x	Cave	Tham Young Chang cave, Muang district, Phang Nga province
<i>Samarplax principe</i> Husana, Tan and Kase, 2011 (Husana et al., 2011)					x					x	Anchialine cave	Principe cave, Eastern Visayas, Samar
<i>Sesarmoides cerberus</i> (Holthuis, 1964)					x					x	Cave	Cave, Nusa Lan island
<i>Sesarmoides emdi</i> Ng and Whitten, 1994					x					x	Cave	Gua Paon cave, Nusa Penida island
<i>Sesarmoides jacobsoni</i> (Ihle, 1912)					x					x	Cave	Guwa Djamblang cave, Guwa Ningmg caves, Bedajo district, Gunung Sewu, Java
<i>Stygotelphusa bidens</i> (Lanchester, 1900)					x					x	Cave	Bau caves in the region of Bau and Sarawak, Borneo
<i>Sundatelphusa cavernicola</i> Takeda, 1983					x					x	Cave	Quinapongan cave, Ughob cave, Antequera, Bohol island
<i>Sundatelphusa boeri</i> Ng and Sket, 1996 (Ng and Sket, 1996)					x					x	Cave	Castigio cave, Caprio springs and rivers near Batuan, Bohol island
<i>Sundatelphusa hades</i> Takeda and Ng, 2001 (Takeda and Ng, 2001)					x					x	Cave	Latay cave, Agusan del Sur, Surigao del Sur, Mindanao
<i>Sundatelphusa lobø</i> Husana, Naruse and Kase, 2009					x					x	Cave	Lobo cave, Samar, Jibong
<i>Sundatelphusa sotoae</i> Ng and Sket, 1996 (Ng and Sket, 1996)					x					x	Cave	Cave, well Ughob cave, Bonigan cave, well, Batuan, Bohol island

To be continued on next page.

Tab. 3. Continued from previous page.

Taxa	Country	Cambodia	Indonesia	Laos	Malaysia	Myanmar	Philippines	Thailand	Vietnam	Habitat	Location
<i>Sundadephusa urichie</i> Ng and Sket, 1996 (Ng and Sket, 1996)		x								Cave	Quilas cave, Batuan, Bohol island
<i>Sundadephusa vedeniki</i> Ng and Sket, 1996 (Ng and Sket, 1996)			x							Cave	Bikahan cave, Antequera, Bohol island
<i>Sundadephusa waray</i> Husana, Naruse and Kase, 2009				x						Cave	Langun cave, Samar, Calbiga
<i>Thephusula bidens</i> (Lanchaster, 1900)				x						Cave	Caves at Bidi, Posih cave, Jambusan cave, Fairy cave, near Bau
<i>Thephusula styx</i> Ng, 1989				x						Cave	Bat cave, Gunung Mulu National Park, Sarawak, Borneo
Acari/Hydrachnida (1 taxon)											
<i>Soldanellonyx monardi sarangensis</i> Viets, 1929		x									
Coleoptera (1 taxon)								x			
<i>Stanoporus deharvengi</i> Spangler, 1996										Cave	Tham Pulu cave, Muang district, Phang Nga province; Tham Kubio cave, Chum Phae district, Khon Kaen province
Pisces (15 taxa)								x			
<i>Barbus speleops</i> Roberts, 1991									x		
<i>Caecogobius cryptophthalmus</i> Bertti and Ercolini, 1991						x				Cave	Chaiyaphum province
<i>Cryptotora thamicola</i> (Kottelat, 1988)						x	x				Cave on Samar island
<i>Clarias niethoffii</i> Valenciennes, 1840				x						Cave	Pang Ma Pha district, Mae Hong Son province
<i>Monopterus albus</i> (Zuilew, 1793) (rice-field eel)						x				Cave	Clearwater cave, Snake cave, Gunung Mulu National Park, Sarawak, Borneo
<i>Nemacheilus ocellatus</i> Kottelat, 1988						x	x				Several caves along the country
<i>Nemacheilus troglotarctes</i> Kottelat and Géry, 1989						x	x				Tham Wang Badan cave, Sai Yok district, Kanchanaburi province
<i>Neolissochilus subterraneus</i> Vidithayanon and Kottelat, 2003						x				Cave	Tham Phra Wang Daeng cave, Noen Maprang district, Phitsanulok province
<i>Pterocryptis buccata</i> Ng and Kottelat, 1998						x				Cave	Sai Yok Noi cave, Sai Yok district, Kanchanaburi province
<i>Puntius microps</i> (Günther, 1868)					x					Cave	Djambiang cave, Bedjo district, Gunung Sewi, Java
<i>Schistura deansmarii</i> Vidithayanon and Kottelat, 2003					x					Cave	Tham Phra Sai Ngam cave, Noen Maprang district, Phitsanulok province
<i>Schistura jarutanini</i> Kottelat, 1990					x					Cave	Sao Hin cave, Thong Pha Phum district, Kanchanaburi province
<i>Schistura spekuli</i> Kottelat, 2004						x					Tam Duong cave, Lai Chau province
<i>Schistura spiesi</i> Vidithayanon and Kottelat, 2003						x					Tham Phra Wang Daeng cave, Noen Maprang district, Phitsanulok province
<i>Silurus furnessi</i> = <i>Pterocryptis furnessi</i> (Fowler, 1905)					x					Cave	Logan's cave, Sarawak, Borneo
<i>Troglocyclocheilus khammouaeensis</i> Kottelat and Bréhier, 1999										Cave	Spring Nam Dön, Thakhek district, Khammouane province
Total: 122 species		3	20	2	19	1		35	36	10	

Names of species and genera are as published in original papers; no taxonomic revisions are included in this analysis.

One-hundred and one species from the list of stygobionts in SE Asia living in karstic habitats are recorded from caves (8 of them from anchialine caves), four species are recorded from karstic springs and one from a thermal spring. Two species were found both in caves and wells, while only one was found from a well. In addition, 13 species were recorded only from porous aquifers (*i.e.* interstitial/hyporheic environment), where *micro-crustaceans* (body size ≤ 1 mm) prevailed. In contrast to porous environments, in karstic caves and springs a wide array of body size could be found – from small-body sized Nematoda and Copepoda (body size < 1 mm) to large-body sized organisms like Decapoda and Pisces (body size > 10 cm).

Historical overview and present status in Thailand

Revision of biospeleological studies and the cave-dwelling fauna of Thailand has been previously done by Deharveng and Bedos (2001) and more recently the terrestrial cave-dwelling fauna was reviewed by Ellis (2006, 2012). Investigations on cave-dwelling fauna have been carried out since the early 20th century but focussed only on terrestrial fauna from some caves in southernmost Thailand (Annandale *et al.*, 1913). *Stenasellus brignoli* Pesce and Argano, 1981 was the first stygobiotic species described for Thailand. It was collected from freshwater wells in Phuket province in 1980 (Pesce and Argano, 1981).

After 1983, the number of biospeleological studies increased as French researchers from the *Association Pyrénéenne de Spéléologie* started their caving activities in Thailand. In 2001, when Deharveng and Bedos (2001) provided the list of aquatic cave-dwelling fauna from Thailand, the list included 21 invertebrate and vertebrate species belonging to 9 higher taxonomic groups (Tab. 3). The ecology and biology of more than half of those species were not known (Deharveng and Bedos, 2000). The most abundant on the list were Isopoda (5 species) and the Pisces (6 species). In addition, there were two species of Amphipoda and two of Decapoda. Several groups (flatworms, oligochaetes, copepods, syncarids, thermosbaenaceans and coleopterans) were represented with only one species and all of them were endemic to Thailand (Tab. 3).

After 2000, 14 new stygobiont species were discovered, among them four new species of fish (Vidthayanon and Kottelat, 2003; Kottelat, 2004), which increased the number of stygobiotic fishes in Thailand from six to ten species. In the last 10 years significant progress has been made in research on the groundwater Copepoda (Fig. 2A and 2B). Before then, only one stygobiotic species was known from the freshwater interstitial habitat (*Elaphoidella margaritae*, Pesce and Apostolov, 1985) (Tab. 3). The first cave-dwelling species found in Thailand was *Elaphoidella namn naoensis* Brancelj, Watirooram

and Sanoamuang, 2010 from a cave in Nam Nao National Park (Phetchabun province) (Brancelj *et al.*, 2010) and the most recently described species are *Bryocyclops mae-waensis* Watirooram, Brancelj and Sanoamuang, 2012 (Watirooram *et. al.*, 2012) and two species from the genus *Fierscyclops* published in this volume (Boonyanusith *et. al.*, 2013). Three papers with descriptions of six new species (but not included in this analysis) have been already submitted to journals (Boonyanusith, personal communication; Watirooram, personal communication). Intensive research on cave environments, especially on epikarst, conducted during the PhD studies of two of the co-authors (CB and SW), revealed that stygobiotic fauna is very rich and not only present in Thailand but also in nearby countries (Vietnam and Laos) (Fig. 2C-G). It includes, apart from the Copepoda also Ostracoda, Syncarida, Isopoda and Amphipoda.

Structure of stygobiotic fauna in Southeast Asia

Thirteen higher taxonomic groups have been recorded so far in SE Asia (including vertebrates, *i.e.* fish; Tab. 3). The most abundant groups so far are the Decapoda (Natantia, Reptantia and Brachyura), represented by 33 taxa (6+3+24 species, respectively), followed by Copepoda (22 species), Isopoda (20 species), Amphipoda (13 species), Pisces (10 species) and Syncarida (5 species). Other groups (Turbellaria, Nematoda, Oligochaeta, Ostracoda, Thermosbaenacea, Acari/Hydrachnida and Coleoptera) are represented only with one to four species each. Out of 74 genera with stygobionts, there are 56 genera where only one stygobiotic representative is known.

The number of species per certain group within a particular country varies considerably – from 1 to 17 (Tabs. 3 and 4). The group with the highest number of species per country is the Decapoda in the Philippines, where 17 species are known, followed by ten species of Copepoda from Thailand. Groups with seven species each per county are the Amphipoda from the Philippines, the Decapoda from Malaysia and the Isopoda from Thailand. Four groups have six representatives per country: Copepoda in the Philippines, Isopoda in Indonesia, Decapoda in Indonesia and the Pisces in Thailand. The group with five species is Copepoda in Vietnam, while Isopoda has four species in the Philippines. There are 29 groups with only one or two species known for each group and for each country.

The time series of stygobiotic records indicates that there are 41 papers, where 48 authors (alone or as co-authors) contributed one single record on stygobiotic fauna; 17 of the records were published before 1980. The rest of the records were contributions by 30 authors who recorded/described two or more new species (Tab. 5). Among those, two records by the same author were done in 1900 (Lanchester, Decapoda) and additional two in 1967 (Borutzky, Copepoda). Up to 1986, 15 more records

Tab. 4. Number of stygobiotic species per higher taxonomic group per country.

	Cambodia	Indonesia	Laos	Malaysia	Myanmar	Philippines	Thailand	Vietnam
Species (n)	3	20	2	19	1	35	36	10
Groups (n)	2	8	2	9	1	6	10	4
Turbellaria		1		2			1	
Nematoda				1				
Oligochaeta							1	
Ostracoda		1		1				
Copepoda		2		1		6	10	5
Syncarida				2			1	2
Isopoda	2	6		2		4	7	
Amphipoda		2		1		7	2	1
Thermosbaenacea	1						2	
Decapoda		6	1	7		17	2	
Acari/Hydrachnida		1						
Coleoptera							1	
Pisces		1	1	2	1	1	9	1

Tab. 5. Authors who published papers on stygofauna from Southeast Asia and their contribution to the knowledge of a particular group (most of them as author or co-author of taxonomic papers) (for details on recorded taxa see Tab. 3).

Author - no. of taxa recorded	Group(s) studied	Author - no. of taxa recorded	Group(s) studied
Ng - 13	Decapoda, Pisces	Mura - 1	Copepoda
Magniez - 12	Isopoda	Rouch - 1	Copepoda
Kottelat - 10	Pisces	Schminke - 1	Syncarida
Brancelj - 7	Syncarida, Copepoda	Andreev - 1	Isopoda
Husana - 7	Decapoda	Argano - 1	Isopoda
Cottarelli - 6	Copepoda	Bruce - 1	Isopoda
Holthuis - 6	Decapoda	Coleman - 1	Isopoda
Sket - 6	Decapoda, Ampipoda, Isopoda	Hosse - 1	Isopoda
Botosaneanu - 5	Ampipoda, Isopoda	Pantivong - 1	Isopoda
Sanoamuang - 5	Copepoda	Rahmadi - 1	Isopoda
Watiroymram - 5	Syncarida, Copepoda	Weagle - 1	Isopoda
Stock - 5	Amphipoda	Boxshall - 1	Amphipoda
Bruno - 4	Copepoda	Chilton - 1	Amphipoda
Kase - 4	Decapoda	Coineau - 1	Amphipoda
Cai - 3	Decapoda	Holsinger - 1	Amphipoda
Camacho - 3	Syncarida	Jaume - 1	Amphipoda
Ilife - 3	Isopoda	Noteboom - 1	Amphipoda
Kawakatsu - 3	Turbellaria	Rao - 1	Amphipoda
Naruse - 3	Decapoda	Sawicki - 1	Amphipoda
Takeda - 3	Decapoda	Schellenberg - 1	Amphipoda
Vidthayanon - 3	Pisces	Cals - 1	Thermosbaenaceaee
Borutzky - 2	Copepoda	Balss - 1	Decapoda
Boutin - 2	Thermosbaenaceaee, Isopoda	Borradaile - 1	Decapoda
Bowman - 2	Isopoda	Goh - 1	Decapoda
Chang - 2	Copepoda	Ihle - 1	Decapoda
Fosshagen - 2	Copepoda	Tan - 1	Decapoda
Mitchell - 2	Turbellaria	Whitten - 1	Decapoda
Pesce - 2	Isopoda, Copepoda	Yeo - 1	Decapoda
Ruffo - 2	Amphipoda	Viets - 1	Acari
Tran - 2	Copepoda	Spangler - 1	Coleoptera
Ball - 1	Turbellaria	Berti - 1	Pisces
Chapman - 1	Turbellaria	Bréhier - 1	Pisces
De Man - 1	Nematoda	Ercolini - 1	Pisces
Yamaguchi - 1	Oligochaeta	Fowler - 1	Pisces
Fernando - 1	Ostracoda	Géry - 1	Pisces
Klie - 1	Ostracoda	Günther - 1	Pisces
Victor - 1	Ostracoda	Roberts - 1	Pisces
Apostolov - 1	Copepoda	Valenciennes - 1	Pisces
Kiefer - 1	Copepoda	Zuiwei - 1	Pisces

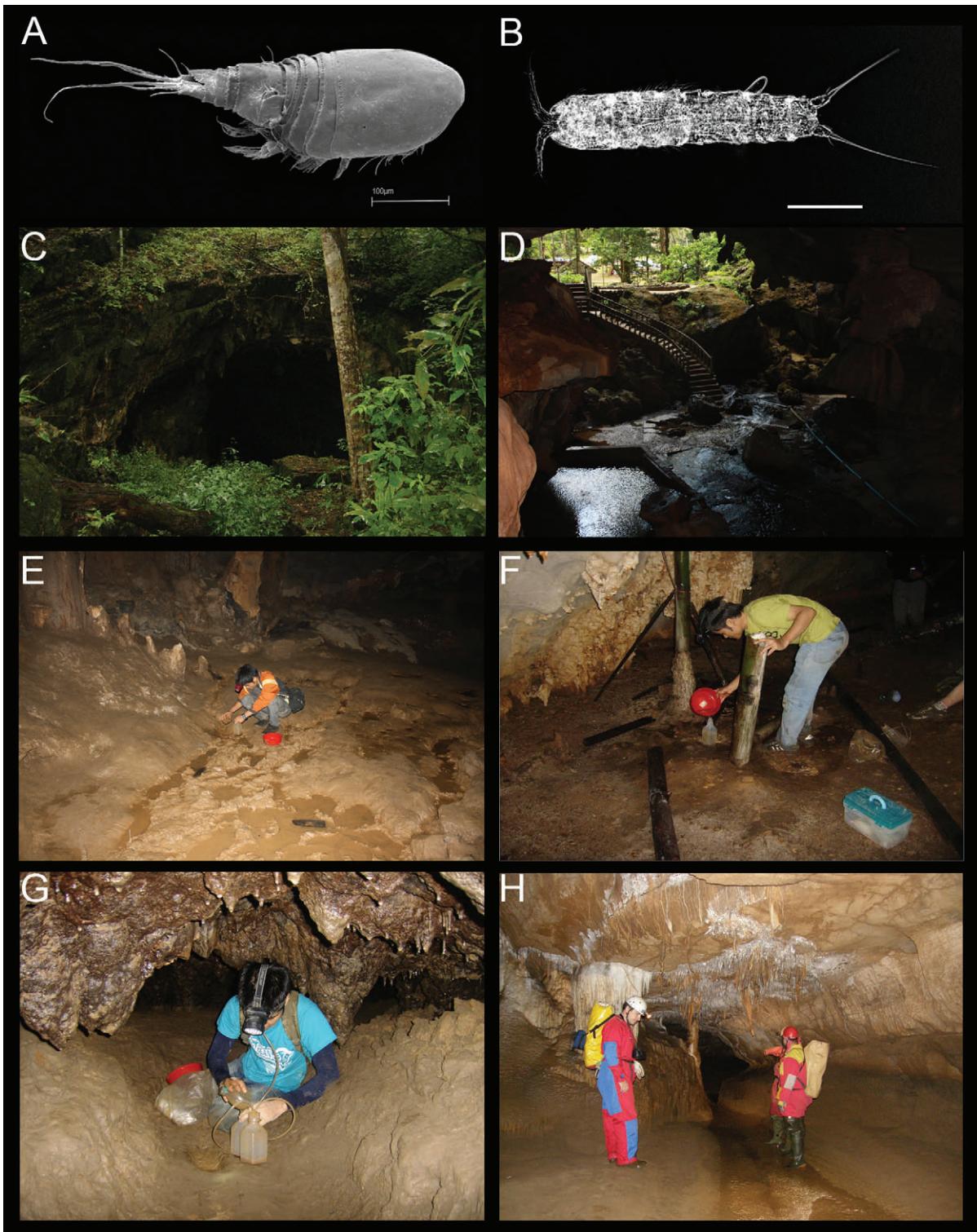


Fig. 2. Epikarst stygobionts and habitats in Southeast Asia. A) Scanning electron microscopy image of a female representative of epikarst copepods, from the order Cyclopoida - *Bryocyclops maewaensis* Watiroyram, Brancelj and Sanoamuang, 2012 (photo by Santi Watiroyram); B) light microscopy image of a female representative of the epikarst copepods, from the order Harpacticoida – *Paramorariopsis irenae* Brancelj, 2006 (photo by Anton Brancelj); C) entrance into a karstic cave (view from outside) in Thailand (photo by Santi Watiroyram); D) entrance into a karstic cave (view from inside) from Laos (photo by Anton Brancelj); E,F,G) sampling of the epikarst fauna from the pools filled by percolating water in caves in Thailand (photo by Santi Watiroyram); H) a detail from a comparable ecosystem (karstic cave) in Slovenia (photo by Anton Brancelj).

were recorded by 7 authors. After 1986, 67 new species were added by authors, who contributed more than two descriptions of a new species. The greatest contributions were by Ng and Martinez – 13 and 12 descriptions, respectively – on Decapoda, Pisces and Isopoda.

DISCUSSION

The first exploration of the freshwater cave fauna in SE Asia started at the end of the 19th century and was mainly limited to terrestrial habitats (Price, 2004). Actually, even today, most work is still focussed on terrestrial fauna (=troglobionts) (Juberthie and Decu, 2001). Some limited exploration was done also on aquatic fauna in the caves. Among the first explorations were those in the Philippines (in 1820), followed by Myanmar (in 1888), Vietnam (in 1906), Indonesia (in 1910), Thailand (in 1913) and Laos (in 1919) (Botosaneanu, 1986). Research on cave fauna in Cambodia and Malaysia started later, in 1960/1961 (Annandale *et al.*, 1913; Botosaneanu, 1986).

Tropical and subtropical karstic areas worldwide were for a long time neglected as suitable places for collecting and studying stygobionts. When comparing Europe (an area of 10,180,000 km² and about 2000 stygobionts) and SE Asia (an area of about 4,304,000 km² and 122 stygobionts), it is obvious that there is a big potential for more stygobionts to be found in SE Asia. A comparison of the number of stygobionts in SE Asia *vs* the rest of the world,

and *vs* the total number of members of particular groups in freshwater, revealed that the number of stygobionts in SE Asia compared with the rest of the world is (still) relatively low (Tab. 6). The only exception is Brachyura (Decapoda), for which the number of stygobionts has significantly increased in the last 25 years. Comparing the area of SE Asia and the rest of the world and number of stygobionts from interstitial and karstic aquifers already known in the rest of the world, at least 800 stygobionts could be expected in SE Asia. The actual numbers of stygobionts recorded for Europe and SE Asia are a combination of stygobionts in fissured (*i.e.* karstic) as well as porous (*i.e.* alluvium; interstitial) aquifers. As both types are common in SE Asia, the estimated number of 800 stygobionts is quite probable and could even be exceeded. In addition to exclusively freshwater caves, there are also numerous anchialine caves along the coasts, which are rich in freshwater, brackish and marine stygobionts (Fosshagen and Ilife, 1989; Husana *et al.*, 2009; Tran and Chang, 2012).

A high potential for discovery of new stygobionts is also indicated by the cumulative curve of stygobiotic taxa over time, which is still very steep and where, in the last 40 years (after 1970), the number of stygobionts increased almost six-fold (from 19 to 122 species) (Fig. 1). The increase of species within a particular group is uneven and reflects mainly the interests and intensity of work by individual authors on the specific group. Currently, the most

Tab. 6. List of the main groups of crustaceans and fish, with the number of known taxa in subterranean habitats in Southeast Asia, worldwide and in all inland surface habitats.

Crustaceans and fish fauna	Southeast Asia*	Stygobionts	Worldwide [°]	World inland water bodies [#]	References
Cladocera	0	5		620	Forró <i>et al.</i> (2008)
Ostracoda	2	119		1936	Martens <i>et al.</i> (2008)
Copepoda	20	607		2774	Boxshall and Defaye (2008)
<i>Calanoida</i>	1	11		552	
<i>Harpacticoida</i>	17	441		1124	
<i>Cyclopoida</i>	2	153		1096	
<i>Gelyelloida</i>	0	2		2	
Syncarida	5	154		240	Camacho and Valdecasas (2008)
Isopoda	21	553		994	Wilson (2008)
Amphipoda	13	665		1870	Väinölä <i>et al.</i> (2008)
Thermosbaenaceae	1+1?	10		18	Jaume (2008)
Decapoda	33	121		2844	
<i>Anomura</i>	0	2		63	Bond-Backup <i>et al.</i> (2008)
<i>Brachyura</i>	24	15		1476	Yeo <i>et al.</i> (2008)
<i>Natantia</i>	6	42 (69 [§])		655	De Grave <i>et al.</i> (2008)
<i>Reptantia</i>	3	31		640	Crandall and Buhay (2008)
Pisces	16	92		12,470	Lêvêque <i>et al.</i> (2008)

*Data from this paper; °data from Botosaneanu, 1986; #see references in right column; §after De Grave *et al.* (2008).

intensively studied groups are the Copepoda, Isopoda, Amphipoda, Decapoda and Pisces, while some other groups, which are well studied elsewhere, are underestimated in SE Asia. Among those groups are the Oligochaeta, Ostracoda and Hydrachnida, represented by only a few species (Tabs. 3 and 5). The effect of highly motivated taxonomists can be seen, for example, in the case of the Indian stygofauna, where a significant increase in the knowledge of *micro-crustaceans* was achieved in relatively short period by only a few specialists (Ranga Reddy and Defaye, 2008; Ranga Reddy *et al.*, 2008; Ranga Reddy and Schminke, 2009). The same is valid for China, where research on karst systems resulted in the description of several new stygobionts (Sket and Fišer, 2009) (Tab. 5). Although both countries, India and China, have high potential for groundwater fauna, there is a slight possibility of sharing common fauna with SE Asia on the species level, except on a very local scale. Based on the present knowledge of the distribution of groundwater fauna in SE Asia, distribution of particular species is rather limited and is usually confined to a region. Only some exceptionally species have *trans-border* distributions over several provinces or countries.

Recent intensive inventory of fauna from relatively unknown environments (*i.e.* epikarst) in Thai caves, has resulted in the discovery of one species of bathynellid and six species of copepods as well as several species of Harpacticoida and Cyclopoida that are not yet described (Brancelj *et al.*, 2010; Camacho *et al.*, 2011; Watiroyram *et al.*, 2012; Boonyanusith *et al.*, 2013; Watiroyram *et al.*, 2013). Along with the true stygobionts from epikarst, many species of Copepoda were collected from pools or streams, but the majority were stygoxenes or stygophiles transported into the caves during floods or as regular drift (Boonyanusith, personal communication; Watiroyram, personal communication). The problem of identifying the correct ecological position of species found in the caves is that specimens can become pale after some time in subterranean environments, which leads to misinterpretation of the stygobiotic nature of collected specimens. Such an example was *Argyrodiaptomus cavernicolax* Shen and Tai, 1965, from a cave in Southern China, which recently appeared to actually be two closely related species of *Sinodiaptomus*, which freely move in and out of the cave (Dumont, personal communication). Another example is *Mesocyclops francisci* Hołyńska, 2000, which was collected from a cave in Northern Thailand (Watiroyram, 2012) but was previously recorded in Malacca, Malaysia, Sumatra and Cambodia from surface water habitats (Hołyńska, 2000; Chaicharoen, 2011). Food in subterranean habitats is an important element that determines population size and biodiversity in temperate zones (Culver *et al.*, 2006). As primary production in tropical zones is more intense, more food is available, especially at the

entrances of the caves, where litter or drift can accumulate. For this reason, Decapoda, especially Brachyura, were frequently reported from those zones in the past as stygobionts when in fact some of them were stygoxenes or stygophiles (Leclerc *et al.*, 2001). However, they contributed to the overall biodiversity of subterranean habitats. For that reason, the distinction between stygophiles and stygobionts is more blurred in the tropical zones when compared to that in temperate zones.

Due to the low intensity of research on fauna in many aquifers worldwide, the distribution of the majority of taxa is still very poorly known. As most stygobionts were found in one or a few sampling campaigns and/or in one or a few locations only, most of them are considered as endemics while in reality they might not be. Scarcity of data on their distribution can lead to the wrong conclusion that all stygobionts are endemic on a small scale (*i.e.* narrow endemics) (Deharveng *et al.*, 2009). Some data about a few species from SE Asia indicates that their range of distribution can be extended at least over two countries (examples in groups of Copepoda, Thermosbaenacea and Decapoda). An example of misinterpretation of endemism can be found in the Copepoda from epikarst in Thailand. After five years of intensive sampling it appears that *rare* and *endemic* taxa are actually quite common – but limited to specific habitats (Brancelj *et al.*, 2010; Watiroyram, 2012; Watiroyram *et al.*, 2012). This supports the idea to put more effort into searching for representatives of some aquatic groups, which are common in surface water bodies but still rare in groundwater, either in porous or karstic aquifers. The most appropriate candidates are groups of Cladocera and Calanoida. Both groups have many representatives in epigean water bodies, while in groundwater they are represented by only a few species (Brancelj and Dumont, 2007). So far, there is only one known stygobiotic species of Calanoida from SE Asia (Brancelj, 2005). Cladocera are represented with representatives from the genus *Nicsmirnovius*, which lives in rheic and hyporheic conditions, much like *Phreatalona*, yet it is not a stygobiont (Van Damme *et al.*, 2003).

For that reason, more intensive and systematic sampling programmes should be prepared for different habitats in interstitial as well as karstic aquifers. Special attention should be put on sampling techniques and equipment. In principle, all sampling methods already known and used in caves and alluvium in Europe and North America (hand-nets, drift nets, plankton nets, baited traps, Bou-Rouch pump and Karaman-Chappuis method) (for details see: PASCALIS protocol) can be applied in the caves and gravel bars of SE Asia. In the past incorrect sampling devices (especially nets with too coarse mesh size) resulted in a loss of many smaller stygobionts. When new techniques were introduced, the number of collected species/specimens increased significantly (Brancelj,

2003). One of the new techniques, specific for SE Asia, is sampling epikarst fauna from *Buddha pots* (Brancelj *et al.*, 2010). They are actually plastic or metal buckets, placed near Buddha statues in the caves to collect dripping water from the ceiling. They appeared as very efficient sampling devices for sampling epikarst fauna and where several new species of Copepoda had been already collected (Brancelj *et al.*, 2010; Watiroyram *et al.*, 2012; 2013).

CONCLUSIONS

In conclusion, faunistic inventories and taxonomic work done on subterranean fauna in SE Asia in the last two decades have revealed that stygobionts are much more common than was thought before. Their number will increase considerably when greater efforts are oriented towards subterranean aquifers.

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