J. Limnol., 2013; 72(s2): 327-344
DOI: 10.4081/jlimnol.2013.s2.e16

The groundwater-dwelling fauna of South East Asia

Anton BRANCELJ,[1,2*] Chaichat BOONYANUSITH,[3] Santi WATIROYRAM,[4] La-orsri SANOAMUANG[3,5]

[1]National Institute of Biology, Večna pot 111, 1000 Ljubljana; [2]Faculty for Environmental Sciences, University of Nova Gorica, Vipavska c. 13, 5000 Nova Gorica, Slovenia; [3]Applied Taxonomic Research Center, Faculty of Science, Khon Kaen University, Khon Kaen 40002; [4]Division of Science, Faculty of Liberal Arts and Science, Nakhon Phanom University, Nakhon Phanom 48000; [5]Faculty of Science, Mahasarakham University, Maha Sarakham 44150, Thailand
*Corresponding author: anton.brancelj@nib.si

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 rises 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.

Received: February 2013. Accepted: September 2013.

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* (Zuiew, 1793)] and amphipods [*Gammarus minus* (Say, 1818), *Niphargus puteanus* (C.L. Koch, 1836)], followed by crabs and shrimps [*Orconeces 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 km^2, 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	*Phagocata vitta*	*Dendrocoelum nausicae*	*Phagocata olivacea*
	(Duges, 1830)	Schmidt, 1861	(Schmidt, 1862)
	Europe, the Alps, Balkan	South Europe and Anatolia	Southeast Adriatic coast
Nematoda			
2	*Pseudorhablolaimus limnophilus*	*Thalassoalamus aquaedulcis*	*Criconema minor*
	Soos, 1937	Schneider, 1940	(Scheider, 1940)
	Hungary, Austria	Slovenia	Slovenia
Oligochaeta			
3	*Trichodrilus pragensis*	*Trichodrilus intermedius*	*Trichodrilus cantabrigensis*
	Vejdovsky, 1875	Fauvel, 1903	Beddard, 1908
	Czech lands	France	United Kingdom
Ostracoda			
4	*Pseudocandona eremita*	*Sphaeromicola topsenti*	*Pseudocandona zschokkei*
	(Vejdovsky, 1880)	Paris, 1916	(Wolf, 1919)
	Central and South Europe	France	West and Central Europe
Copepoda			
	Calanoida		
5	*Microdiaptomus cokeri*	*Speodiaptomus birsteini*	*Ridgewayia marki*
	Osorio Tafall, 1942	Borutsky, 1962	(Esterly, 1911) - anchialine,
	Mexico	Krim peninsula (Ukraine)	Bermuda islands
	Cyclopoida		
6	*Diacyclops languidoides*	*Acanthocyclops venustus*	*Eucyclops terras*
	(Lilljeborg, 1901)	(Norman and Scott, 1906)	(Graeter, 1907)
	Europe	Europe	Switzerland
	Harpacticoida		
7	*Parastenocaris fontinalis*	*Bryocamptus pyrenaicus*	*Nitocrella hirta*
	Schnitter and Chappuis, 1915	(Chappuis, 1923)	Chappuis, 1923
	Europe	France, Slovenia	Europe
Syncarida			
8	*Bathynella natans*	*Anaspides tasmaniae*	*Bathynella chappuisi*
	Vejdovsky, 1882	(Thomson, 1893)	Delachaux, 1920
	Europe	Tasmania (Australia)	Europe
Isopoda			
	Cirolanidae		
9	*Cirolanides texensis*	*Spahaeromides raymondi*	*Faucheria faucheri*
	Benedict, 1896	Dollfus, 1897	(Dolphus and Virè, 1900)
	Texas (USA)	France	France
	Sphaeromatidae		
10	*Monolistra caeca*	*Caecosphaeroma virei*	*Caecosphaeroma burgundum*
	Gerstaecker, 1856	Dollfus, 1896	Dollfus, 1896
	Slovenia	France	France
	Anthuridea		
11	*Cruregens fontanus*	*Cyanthura curassavica*	*Cyanthura milloti*
	Chilton, 1881	Stork, 1940	Chappuis, Delamare Deboutteville and Paulian, 1956
	New Zealand	Central America	Reunion island
	Asellota		
12	*Caecidotea stygia*	*Caecidotea nickajackensis*	*Asellus hilgendorfi*
	Packard, 1871	Packard, 1881	Bovallius, 1886
	Central part of USA	Tennessee (USA)	Japan
	Microcerberidae		
13	*Microcerberus stygius*	*Microcerberus remanei*	*Microcerberus delamarei*
	Karaman, 1933	Chappuis and Delamare, 1952	Remane and Siewing, 1953
	Macedonia	Mediterranean area	Brazil
	Phreatoicidea		
14	*Phreatoicus typicus*	*Neophreatoicus assimilis*	*Phreatoicoides gracilis*
	Chilton, 1882	Chilton, 1884	Sayce, 1900
	New Zealand	New Zealand	Australia

To be continued on next page.

Tab. 1. Continued from previous page.

Amphipoda			
Gammaridae			
15	*Gammarus minus* Say, 1818 Central part of USA	*Rhipidogammarus rhipidophorus* (Catta, 1878) Mediterranean area	*Sarathrogammarus guernei* (Chevreux, 1889) Azores (Portugal)
Melitidae			
16	*Eriopsia elongata* (Bruzelius, 1859) Europe, USA	*Eriopsella sechellensis* (Chevreux, 1901) Seychelles	*Pseudoniphargus africanus* Chevereux, 1901 Algeria
Niphargidae			
17	*Niphargus puteanus* (C.L. Koch, 1836) Germany, Switzerland	*Niphargus stygius* (Schiödte, 1847) Slovenia	*Niphargus longicaudatus* A. Costa, 1851 Italy
Crangonyctidae			
18	*Crangonyx subterraneus* Bate, 1859 West and Central Europe	*Stygobromus tenuis* (Smith, 1874) East coast of USA	*Bactrurus mucronatus* (Forbes, 1876) Central part of USA
Thermosbaenacea			
19	*Thermosbaena mirabilis* Monod, 1924 Tunisia	*Monodella stygicola* Ruffo, 1949 Italy	*Monodella argentarii* Stella, 1951 Italy
Decapoda			
Natantia			
20	*Troglocaris anophthalmus* (Kollar, 1848) Slovenia, Italy	*Barbouria cubensis* (Von Martens, 1872) Cuba	*Caridina japonica* De Man, 1892 Japan
Reptantia			
21	*Orconeces pellucidus* (Tellkampf, 1844) Tennessee (USA)	*Orconeces inermis* Cope, 1872 Kentucky, Indiana (USA)	*Cambarus hamulatus* (Cope, 1881) Alabama, Tennessee (USA)
Brachyura			
22	*Thelphusula bidiens* (Lanchester, 1900) Sarawak, Borneo	*Sesarmoides jacobsoni* (Ihle, 1912) Central Java, Indonesia	*Sesarmoides verleyi* (Rathbun, 1914) Jamaica
Acarina			
Hydrachnida			
23	*Wandesia thori* (Schecthel, 1912) Europe	*Frontipodopsis staheli* Walter, 1919 Central and South America	*Sczizobates disjunctus* (Walter, 1925) Argentina
Coleoptera			
24	*Siettitia balsetensis* Abielle de Perrin, 1904 France	*Siettitia avenionensis* Guignot, 1925 France	*Uvarus chappuisi* (Peschet, 1932) Burkina Faso
Pisces			
25	*Taenioides anguillaris* (Linnè, 1758) China	*Monopterus albus* (Zuiew, 1793) Mjanmar, China, Japan	*Trypauchen vagina* (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 subcontinent 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 km^2, 408,000 km^2 (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* (Botosaneanu, 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; Botosaneanu, 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

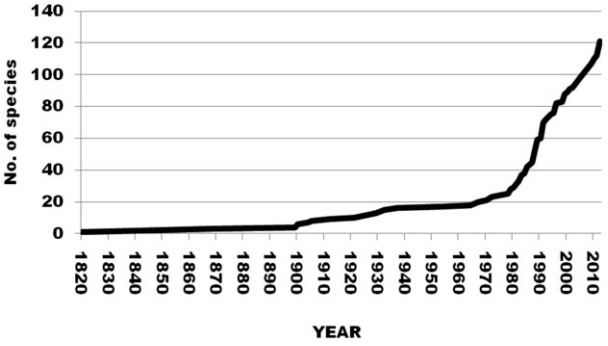

Fig. 1. Cumulative number of stygobiotic taxa recorded in Southeast Asia from 1820 up to 2012.

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

Taxa	Country								Habitat	Location
	Cambodia	Indonesia	Laos	Malaysia	Myanmar	Philippines	Thailand	Vietnam		
Turbellaria (4 taxa)										
Dugesia batuensis Ball, 1970				x					Cave	Batu cave near Kuala Lumpur, Gombak district
Dugesia deharvengi Kawakatsu and Mitchell, 1989							x		Cave	Tham Kubio cave, Chum Phae district, Khon Kaen province Tham Phulu cave, Muang district, Phang Nga province
Dugesia leclerci Kawakatsu and Mitchell, 1995		x							Cave	Gua Tanette cave, Maros island, Sulawesi
Mitchellia sarawakana Kawakatsu and Chapman, 1983				x					Cave	Water Polo cave, Gunung Mulu National Park, Sarawak, Borneo
Nematoda (1 taxon)										
Dorylaiumus selengorensis De Man, ?				x					Cave	Batu caves near Kuala Lumpur, Gombak district
Oligochaeta (1 taxon)										
Haplotaxis glandularis Yamaguchi, 1953							x		Cave	Tham Kubio cave, Chum Phae district, Khon Kaen province
Ostracoda (2 taxa)										
Batucypretta paradoxa Victor and Fernando, 1980				x					Cave	Batu caves near Kuala Lumpur, Gombak district
Candonopsis putealis Klie, 1932		x							Spring	Well, Bogor island
Copepoda (22 taxa)										
Asiacaris dispar Cottarelli, Bruno and Berera, 2010 (Cottarelli *et al.*, 2010)							x		Hyporheic	Than Sadet river, Pha-ngan island, Surat Thani province
Attheyella (Canthosella) vietnamica Borutzky, 1967							x	x	Cave	Cave in NorthVietnam, Lac Thuy district, Hoa Bin province; Tham Bot Wangna cave, Noen Maprang district, Phitsanulok province
Boholina crasicephala Fosshagen, 1989						x			Anchialine cave	San Vicent cave, San Vicente
Boholina purgata Fosshagen, 1989						x			Anchialine cave	San Vicent cave, San Vicente
Bryocyclops maewaensis Watiroyram, Brancelj and Sanoamuang, 2012							x		Cave	Tham Nam Phar Ngam cave, Mae Wa National Park, Mae Phrik district, Lampang province
Elaphoidella bidens decorata (Sars, 1904)		x					x		Cave	Pauh Cave, Bukttinggi; Vijer cave near botanic garden; several caves in Kanchanaburi province
Elaphoidella jaesornenis Watiroyram, Brancelj and Sanoamuang, 2013							x		Cave	Tham Phar Ngam cave, Jaesorn National Park, Wang Nuea district, Lampang province
Elaphoidella margaritae Pesce and Apostolov, 1985 (Pesce and Apostolov, 1985)							x		Well	Wells on Phuket island, Phuket province
Elaphoidella namnaoensis Brancelj, Watiroyram and Sanoamuang, 2010							x		Cave	Tham Yai Nam Nao cave, Nam Nao National Park, Nam Nao district, Phetchabun province
Elaphoidella thailadensis Watiroyram, Brancelj and Sanoamuang, 2013							x		Cave	Tham Khun cave, Noen Maprang district, Phitsanulok province
Elaphoidella vietnamica Borutzky 1967								x	Cave	Cave in North Vietnam, Lac Thuy district, Hoa Bin province
Epactophanes philippinus Bruno and Cottarelli, 1999 (Bruno and Cottarelli, 1999)						x			Interstitial	Phreatic, Matitunao river, Cebu island
Fierscyclops solaris Boonyanusith, Brancelj and Sanoamuang, 2013							x		Spring	Wat Yang Kao temple, Sangkhlaburi district, Kanchanaburi province
Fierscyclops tanasosriensis Boonyanusith, Brancelj and Sanoamuang, 2013							x		Cave	Kaeo Sawan Badan cave, Sangkhlaburi district, Kanchanaburi province

To be continued on next page.

Tab. 3. Continued from previous page.

Taxa	Country								Habitat	Location
	Cambodia	Indonesia	Laos	Malaysia	Myanmar	Philippines	Thailand	Vietnam		
Hadodiaptomus dumonti Brancelj, 2005								x	Cave	Dang Water cave, Cuc Phuong National Park, Ha Noi
Halicyclops thermophilus Kiefer, 1929		x							Therm. spring	Salt thermal spring, Kuripan, Java
Microarthridion thanhi Tran and Chang, 2012								x	Anchialine cave	Cave, Ninh Binh province
Nitocra vietnamensis Tran and Chang, 2012								x	Anchialine cave	Cave, Ninh Binh province
Parastenocaris arganoi Cottarelli and Mura, 1982				x					Cave	Batu caves near Kuala Lumpur, Gombak district
Parastenocaris mangyans Bruno and Cottarelli, 1999 (Bruno and Cottarelli, 1999)						x			Interstitial	Phreatic near Talipanan village, Mindoro island
Parastenocaris distincta Cottarelli, Bruno and Berera, 2006 (Cottarelli *et al.*, 2006)						x			Interstitial	Phreatic, Mindoro island
Phyllognathopus bassoti Rouch, 1972						x			Interstitial	Shore of lake Wisdom, New Guinea
Syncarida (5 taxa)										
Batubathynella malaya (Sars, 1929)				x					Cave	Batu caves near Kuala Lumpur, Gombak district
Paraeobathynella vietnamensis Camacho, 2005 (Camacho, 2005)								x	Cave	Hang Trinh Nu cave, Bo Hon island
Sabahbathynella wongi Schminke, 1988				x					Interstitial	Sungai Masalong river, Sabah, Borneo
Siambathynella laorsriae Camacho, Watiroyram and Brancelj, 2011							x		Cave	Tham Yai Nam Nao cave, Nam Nao National Park, Nam Nao district, Phetchabun province
Sketinella trontelji Camacho, 2005 (Camacho, 2005)								x	Cave	Cave, Rom island
Isopoda (21 taxa)										
Annina fustis (Bowman and Iliffe, 1991)							x		Cave	Tham Rusi cave, Muang district, Phang Nga province
Anopsilana conditoria Bruce and Iliffe, 1992 (Bruce and Iliffe, 1992)						x			Anchialine cave	Cave on islet north of Koron island
Anopsilana lingua Bowman and Iliffe, 1987						x			Anchialine cave	Cave, Palau islands, Republic of Palau
Cyathura (Stygocyathura) chapmani Andreev, 1982				x					Cave	Gua Air Jernih cave, Gunung Mulu National Park; Borneo
Cyathura (Stygocyathura) filipinica Botosaneanu and Sket, 1999 (Botosaneanu and Sket, 1999)						x			Cave, spring	Caesar's cave, well, Batuan, Bohol island
Cyathura (Stygocyathura) papuae Weagle, Coleman and Hosse, 1987 (Weagle *et al.*, 1987)						x			Interstitial	Interstitial 1.3 m deep, Bambu river, Papua New Guinea, Lae Morobe province
Stenasellus bedosae Magniez, 1991							x		Cave	Tham Phanthurat cave in Khao Sok National Park, Phanom district, Surat Thani province
Stenasellus boutini Magniez, 1991	x								Cave	Caves in Batammbang province
Stenasellus brignolii Pesce and Argano, 1981							x		Spring	Spring, Phuket island, Phuket province
Stenasellus cambodianus Boutin and Magniez, 1985	x								Cave	Cave near Kampong Trach district, Kampot province,
Stenasellus chapmani Magniez, 1982				x					Cave	Snake cave, Water Polo cave, New High Level cave, Sarawak, Borneo
Stenasellus covillae Magniez, 1987		x							Cave	Bat Quarry cave, Aceh Besar, Sumatra
Stenasellus deharvengi Magniez, 1991							x		Cave	Tham Keao cave near Nong Bua Daeng, Phakdi Chumphon district, Chaiyaphum province
Stenasellus foresti Magniez, 2002		x							Cave	Ngalau Surat cave, Ngalu Pelayangan cave, Sumatra

To be continued on next page.

Tab. 3. Continued from previous page.

Taxa	Country								Habitat	Location
	Cambodia	Indonesia	Laos	Malaysia	Myanmar	Philippines	Thailand	Vietnam		
Stenasellus javanicus Magniez and Rahmadi, 2006 (Magniez and Rahmadi, 2006)		x							Cave	Cikaray cave, Leuwi Kares island
Stenasellus mongnatei Magniez and Pantivong, 2005 (Magniez and Pantivong, 2005)							x		Cave	Tham Nam cave, Kaeng Khoi district, Saraburi province
Stenasellus monodi Magniez, 2000		x							Cave	Ngalau Lagung cave, Sumatra
Stenasellus rigali Magniez, 1991							x		Cave	Tham Kubio cave, Chum Phae district, Khon Kaen province
Stenasellus stocki Magniez, 2001		x							Cave	Ngalau Indah cave, Sumatra
Stenasellus strinatii Magniez, 1991		x							Cave	Ngalu Baso cave, Ngalau Kamang cave, Sumatra
Thalandoniscus annae Dalens, 1989							x		Cave	Springs near the Tham Tapan cave, Muang district, Phang Nga province
Amphipoda (13 taxa)										
Aequigidiella aquilifera Botosaneanu and Stock, 1989							x		Cave	Tham Phulu cave, Muang district, Phang Nga province; Tham Keao cave, Phakdi Chumphon district, Chaiyaphum province
Bogidiella daccordii Ruffo, 1994						x			Interstitial	Phreatic on Palawan island, St. Paul subterranean river Nat Park, Western Visayas
Bogidiella deharvengi Stock and Botosaneanu, 1988		x							Cave	Batu Lubang cave, Halmashera island
Bogidiella (Medigidiella) sarawacensis Stock, 1983				x					Cave	Niah Great cave, Batu Niah National Park, Sarawak, Borneo; Deer cave, Gunung Mulu National Park, Sarawak, Borneo
Bogidiella thai Botosaneanu and & Noteboom, 1988							x		Cave	Tham Poung Chang cave, Muang district, Phang Nga province
Bollegidia sootai (Coineau and Rao, 1972)						x			Interstitial	Interstitial, Sabang beach, eastern Mindoro, Palawan islands
Cottarellia minima Ruffo, 1994						x			Interstitial	Interstitial, Sabang beach, eastern Mindoro, Palawan islands
Eriopsia philippensis (Chilton, 1921)						x			Well	Well near Los Baños, southern shore of Laguna de Bay, Luzon island
Flagitopsia fluviatilis (Stock, 1991)						x			Interstitial	Pagsanjan falls, Laguna province, Luzon island
Paraniphargus ruttneri Schellenberg, 1931		x							Cave	Batu Lubang cave, Halmahera, east Java
Psammogammarus fluviatilis Stock, 1991						x			Interstitial	Gravel bar near Pagsanjan falls, laguna
Seborgia vietnamica Jaume, Sket and Boxshall, 2009 (Jaume *et al.*, 2009)								x	Cave	Cave Dong Duc Tie, Dao Van Gio island
Tegano barnadi Sawicki and Holsinger, 2005						x			Cave	Airport well cave, Peleliu island
Thermosbaenacea (2 taxa)										
Theosbaena cambodjiana Cals and Boutin, 1985	x						x		Cave	Cave near Kampong Trach district, Kompot province
Thermosbaena sp.							x		Cave	Tham Kubio cave, Chum Phae district, Khon Kaen province
Decapoda (Natantia, Reptatntia and Brachyura) (33 taxa)										
Adelana chapmani (Holthuis, 1979)				x					Cave	Niah Great cave, near Miri, Borneo
Arachnothelphusa rhadamanthysi (Ng and Goh, 1978)				x					Cave	Simud Puteh cave, Sabah, Borneo
Archipelothelphusa cavernicola Takeda, 1983						x			Cave	Quinapon-an cave, Antequera, Bohol island

To be continued on next page.

Tab. 3. Continued from previous page.

Taxa	Country								Habitat	Location
	Cambodia	Indonesia	Laos	Malaysia	Myanmar	Philippines	Thailand	Vietnam		
Archipelothelphusa longipes Balss, 1937						x			Cave	Bautakay cave, Atimonau, Quezon province, Luzon island
Cancrocaeca xenomorpha Ng, 1991 (Ng, 1991)		x							Cave	Gua Tanette cave, Lubang Batu Neraka cave, cave in Maros, Maros, Sulawesi
Cerberusa coeca Holthuis, 1979				x					Cave	Deer cave, Green cave, Clearwater cave, Gunung Mulu National Park, Sarawak, Borneo
Cerberusa tipula Holthuis, 1979				x					Cave	Clearwater cave, cave of Winds, Wonder cave, Gunung Api masiff, Gunung Mulu National Park, Sarawak, Borneo
Edoneus atheatus Holthuis, 1978						x			Cave	Subterranean river near Santiago, Isabela province, Luzon island; cave near Sitio Disiluad, Aglipay Quirino province, Luzon island
Edoneus erwini Cai and Husana, 2009 (Cai and Husana, 2009)						x			Cave	Bantakay cave, Luzon island
Edoneus marulas Cai and Husana, 2009 (Cai and Husana, 2009)						x			Cave	Marulas caves, Luzon island
Edoneus sketi Cai and Husana, 2009 (Cai and Husana, 2009)						x			Cave	Bantakay cave, Luzon island
Erebusa calobates Yeo and Ng, 1999			x						Cave	Tham Tê cave, Thakhek district, Khammouane province
Karstarma philippinarum Husana, Naruse and Kase, 2010 (Husana *et al.*, 2010)						x			Anchialine cave	Bat cave, Boracay island; Tagbaobo cave, Samal island
Macrobrachium poeti Holthuis, 1984		x							Cave	Several caves, probably only in Gunung Sewu Karst
Nemoron nomas Ng, 1996								x	Cave	Cave in Phong Nha, Hang Toi, Quang Binh province
Parhippolyte uveae Borradaile, 1899		x				x			Cave	Tiniguaban cave, Gimaras, Tinigualban island; Holmahera, Maluccas
Phaibulamon stilipes Ng, 1992							x		Cave	Tham Nam Phrah Khoan cave, Sangkhlaburi district, Kanchanaburi province
Phricothelphusa deharvengi Ng, 1988							x		Cave	Tham Poung Chang cave, Muang district, Phang Nga province
Samarplax principe Husana, Tan and Kase, 2011 (Husana *et al.*, 2011)						x			Anchialine cave	Principe cave, Eastern Visayas, Samar
Sesarmoides cerberus (Holthuis, 1964)		x							Cave	Cave, Nusa Lain island
Sesarmoides emdi Ng and Whitten, 1994		x							Cave	Gua Paon cave, Nusa Penida island
Sesarmoides jacobsoni (Ihle, 1912)		x							Cave	Guwa Djamblang cave, Guwa Ningrng caves, Bedojo district, Gunung Sewu, Java
Stygothelphusa bidiensis (Lanchester, 1900)				x					Cave	Bau caves in the region of Bau and Sarawak, Borneo
Sundathelphusa cavernicola Takeda, 1983						x			Cave	Quinaponan cave, Ughob cave, Antequera, Bohol island
Sundathelphusa boex Ng and Sket, 1996 (Ng and Sket, 1996)						x			Cave	Castigio cave, Capiro springs and rivers near Batuan, Bohol island
Sundathelphusa hades Takeda and Ng, 2001 (Takeda and Ng, 2001)						x			Cave	Latay cave, Agusan del Sur, Surigao del Sur, Mindanao
Sundathelphusa lobo Husana, Naruse and Kase, 2009						x			Cave	Lobo cave, Samar, Jiabong
Sundathelphusa sottoae Ng and Sket, 1996 (Ng and Sket, 1996)						x			Cave, well	Ughob cave, Bonugan cave, well, Batuan, Bohol island

To be continued on next page.

Tab. 3. Continued from previous page.

Taxa	Country								Habitat	Location
	Cambodia	Indonesia	Laos	Malaysia	Myanmar	Philippines	Thailand	Vietnam		
Sundathelphusa urichie Ng and Sket, 1996 (Ng and Sket, 1996)						x			Cave	Quilas cave, Batuan, Bohol island
Sundathelphusa vedeniki Ng and Sket, 1996 (Ng and Sket, 1996)						x			Cave	Bikahan cave, Antequera, Bohol island
Sundathelphusa waray Husana, Naruse and Kase, 2009						x			Cave	Langun cave, Samar, Calbiga
Thelphusula bidiens (Lanchaster, 1900)				x					Cave	Caves at Bidi, Posih cave, Jambusan cave, Fairy cave, near Bau
Thelphusula styx Ng, 1989				x					Cave	Bat cave, Gunung Mulu National Park, Sarawak, Borneo
Acari/Hydrachnida (1 taxon)										
Soldanellonyx monardi sarangensis Viets, 1929		x							Spring	Java
Coleoptera (1 taxon)										
Siamoporus deharvengi Spangler, 1996							x		Cave	Tham Pulu cave, Muang district, Phang Nga province; Tham Kubio cave, Chum Phae district, Khon Kaen province
Pisces (15 taxa)										
Barbus speleops Roberts, 1991							x		Cave	Tham Phu Khieo cave, Nong Bua Daeng district, Chaiyaphum province
Caecogobius cryptophthalmus Berti and Ercolini, 1991						x			Cave	Cave on Samar island
Cryptotora thamicola (Kottelat, 1988)							x		Cave	Susa cave, Pang Ma Pha district, Mae Hong Son province
Clarias nieuhofii Valenciennes, 1840				x					Cave	Clearwater cave, Snake cave, Gunung Mulu National Park, Sarawak, Borneo
Monopterus albus (Zuiew, 1793) (rice-field eel)					x				Cave	Several caves along the country
Nemacheilus oedipus Kottelat, 1988							x		Cave	Several caves in Pang Mapha district, Mae Hong Son province
Nemacheilus troglocatarctus Kottelat and Géry, 1989							x		Cave	Tham Wang Badan cave, Sai Yok district, Kanchanaburi province
Neolissochilus subterraneus Vidthayanon and Kottelat, 2003							x		Cave	Tham Phra Wang Daeng cave, Noen Maprang district, Phitsanulok province
Pterocryptis buccata Ng and Kottelat, 1998							x		Cave	Sai Yok Noi cave, Sai Yok district, Kanchanaburi province
Puntius microps (Günther, 1868)		x							Cave	Djamblang cave, Bedojo district, Gunung Sewu, Java
Schistura deansmarti Vidthayanon and Kottelat, 2003							x		Cave	Tham Phra Sai Ngam cave, Noen Maprang district, Phitsanulok province
Schistura jarutanini Kottelat, 1990							x		Cave	Sao Hin cave, Thong Pha Phum district, Kanchanaburi province
Schistura spekuli Kottelat, 2004								x	Cave	Tam Duong cave, Lai Chau province
Schistura spiesi Vidthayanon and Kottelat, 2003							x		Cave	Tham Phra Wang Daeng cave, Noen Maprang district, Phitsanulok province
Silurus furnessi = *Pterocryptis furnessi* (Fowler, 1905)				x					Cave	Logan's cave, Sarawak, Borneo
Troglocyclocheilus khammouaensis Kottelat and Bréhier, 1999			x						Cave	Spring Nam Dôn, 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 namnaoensis* Brancelj, Watiroyram 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 maewaensis* Watiroyram, Brancelj and Sanoamuang, 2012 (Watiroyram *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; Watiroyram, 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 (Turbellia, 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	1
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	Amphipoda, Isopoda	Pantivong - 1	Isopoda
Sanoamuang - 5	Copepoda	Rahmadi - 1	Isopoda
Watiroyram - 5	Syncarida, Copepoda	Weagle - 1	Isopoda
Stock - 5	Amhipoda	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	Thermosbaeanaceae
Borutzky - 2	Copepoda	Balss - 1	Decapoda
Boutin - 2	Thermosbaeanaceae, 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	Zuiew - 1	Pisces

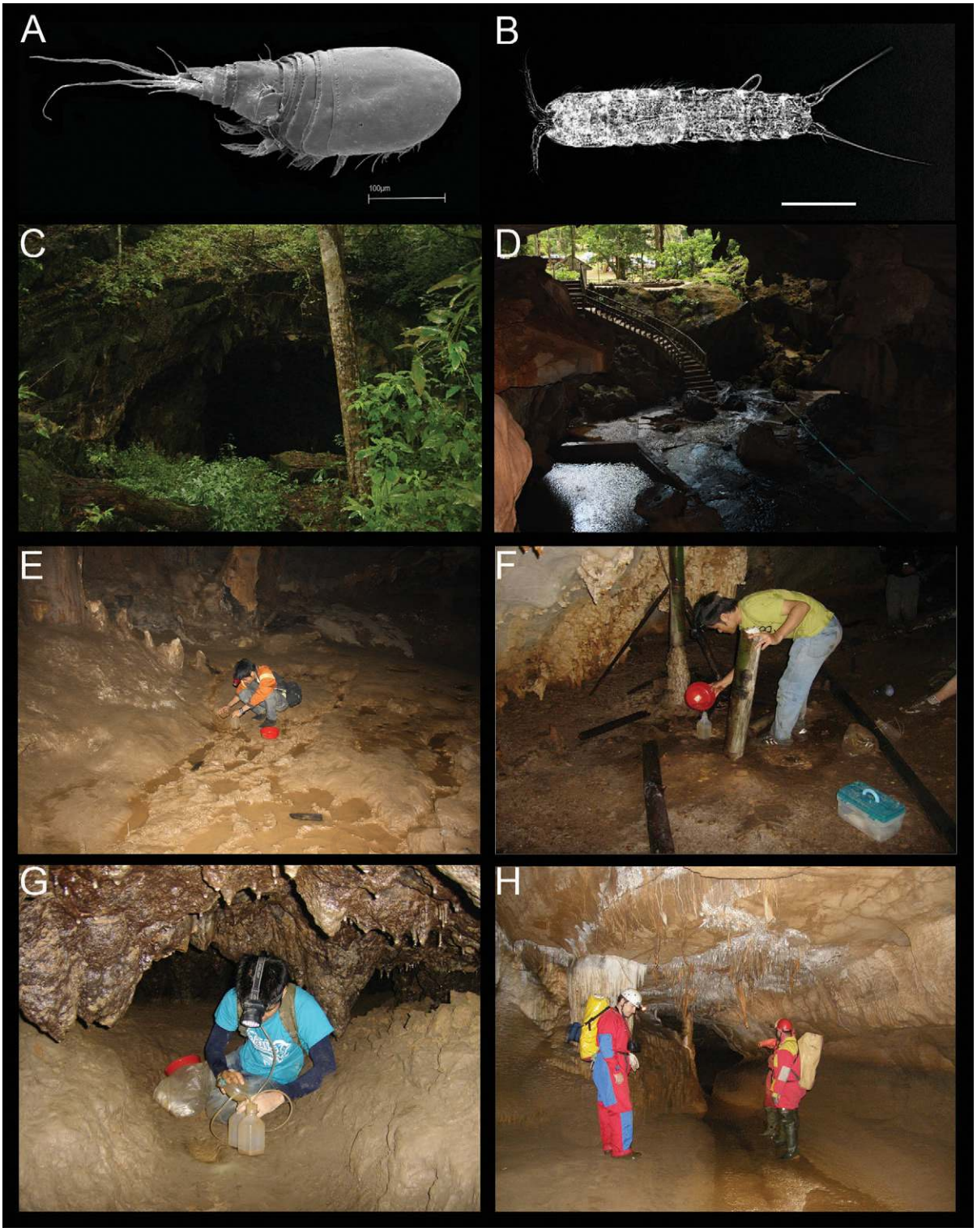

Fig. 2. Epikarst stygobionts and habitats in Southeast Asia. A) Scanning electron microscopy image of a female representative of epikarst copepods, from the order Cyclopoida - *Bryocyclops maewaensis* Watiroyram, Brancelj and Sanoamuang, 2012 (photo by Santi Watiroyram); B) light microscopy image of 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 epikarstic 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 km^2 and about 2000 stygobionts) and SE Asia (an area of about 4,304,000 km^2 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	Stygobionts		World inland water bodies[#]	References
	Southeast Asia[*]	Worldwide[°]		
Cladocera	0	5	620	Forró *et al.* (2008)
Ostracoda	2	119	1936	Martens *et al.* (2008)
Copepoda	20	607	2774	Boxshall and Defaye (2008)
Calanoida	1	11	552	
Harpacticoida	17	441	1124	
Cyclopoida	2	153	1096	
Gelyelloida	0	2	2	
Syncarida	5	154	240	Camacho and Valdecasas (2008)
Isopoda	21	553	994	Wilson (2008)
Amphipoda	13	665	1870	Väinölä *et al.* (2008)
Thermosbaenaceae	1+1?	10	18	Jaume (2008)
Decapoda	33	121	2844	
Anomura	0	2	63	Bond-Backup *et al.* (2008)
Brachyura	24	15	1476	Yeo *et al.* (2008)
Natantia	6	42 (69[§])	655	De Grave *et al*. (2008)
Reptantia	3	31	640	Crandall and Buhay (2008)
Pisces	16	92	12,470	Lêvêque *et al.* (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.

ACKNOWLEDGMENTS

We thank Martin Ellis who supplied the list of organisms found in karstic areas and subterranean habitats in Thailand. This work was partly supported by the National Research University Project of Thailand, Office of the Higher Education Commission, through the Holistic Watershed Management Cluster of Khon Kaen University. The senior author (AB) would like to thank to the organisers of the FISA conference for invitation to the meeting. The authors wish to thank Dr. Jolyon Dodgson for his help with the English corrections and two anonymous reviewers for their useful comments on the earlier version of the paper.

REFERENCES

Annandale N, Brown JC, Gravely FH, 1913. The limestone caves of Burma and the Malay Peninsula. J. Asiat. Soc. Bengal 9:391-423.

Bond-Backup G, Jara CG, Pérez-Losada M, Backup L, Crandall KA, 2008. Global diversity of crabs (Aeglidae: Anomura: Decapoda) in freshwater. Hydrobiologia 595:267-273.

Boxshall GA, Defaye D, 2008. Global diversity of Copepods (Crustacea: Copepoda) in freshwater. Hydrobiologia 595: 195-207.

Botosaneanu L, 1986. Stygofauna mundi. A faunistic, distributional and ecological synthesis of the world fauna inhabiting subterranean waters (including the marine interstitial). Brill Publ., Leiden: 740 pp.

Botosaneanu L, Sket B, 1999. A new freshwater stygobiotic species of *Cyathura* (Isopoda: Anthuridae) from Bohol Island, the Philippines. Acta Biol. Slov. 42:27-33.

Boonyanusith C, Brancelj A, Sanoamuang L, 2013. New representatives of the genus *Fierscyclops* Karanovic, 2004 (Copepoda, Cyclopidae) from South East Asia. J. Limnol. 72(Suppl.2):e13.

Brancelj A, 2003. Biological sampling methods for epikarst water. In: W.K. Jones, D.C. Culver and J.S. Herman (eds.), Proc. Symp. Epikarst. Karst Waters Institute Publ.

Brancelj A, 2005. *Hadodiaptomus dumonti* n. gen., n. sp., a new freshwater stygobiotic calanoid (Crustacea: Copepoda: Calanoida) from Vietnam (South Asia) and a new member of the subfamily Speodiaptominae Borutzky, 1962. Hydrobiologia 534:57-70.

Brancelj A, Dumont HJ, 2007. A review of diversity, adaptations and groundwater colonization pathways in Cladocera and Calanoida (Crustacea), two rare and contrasting groups of stygobionts. Fund. Appl. Limnol. 168:3-17.

Brancelj A, Watiroyram S, Sanoamuang L, 2010. The first record of cave-dwelling Copepoda from Thailand and description of a new species: *Elaphoidella namnaoensis* n. sp. (Copepoda, Harpacticoida). Crustaceana 83:779-793.

Bruce NL, Iliffe TM, 1992. *Anopsilana conditoria,* a new species of anchialine troglobitic cirolanid isopod (Crustacea) from the Philippines. Stygologia 7:225-230.

Bruno MC, Cottarelli V, 1999. Harpacticoids from groundwaters in the Philippines: *Parastenocaris mangyans*, new species, *Epactophanes philippinus*, new species, and redescription of *Phyllognathopus bassoti* (Copepoda). J. Crustacean Biol. 19:510-529.

Cai YX, Husana DEM, 2009. Cave shrimps of the genus *Edoneus* Holthuis, 1978, from Luzon, the Philippines, with description of three new species (Crustacea: Decapoda: Atyidae). Raffles B. Zool. 57:51-63.

Camacho AI, 1992. The natural history of biospeleology. Museo Nacional de Cicencas Naturales ed., Madrid: 374 pp.

Camacho AI, 2005. Disentangling an Asian puzzle: two new bathynellid (Crustácea, Syncarida, Parabathynellidae) genera from Vietnam. J. Nat. Hist. 39:2861-2886.

Camacho AI, Valdecasas AG, 2008. Global diversity of Syncarids (Syncarida; Crustacea) in freshwater. Hydrobiologia 595:257-266.

Camacho AI, Watiroyram S, Brancelj A, 2011. The first record of Bathynellacea from Thailand: a new genus and species of Parabathynellidae (Crustacea: Syncarida). J. Nat. Hist. 45:45-46.

Chaicharoen R, 2011. Diversity and distribution of freshwater calanoid and cyclopoid copepods in seven provinces of Cambodia. PhD Thesis. Khon Kaen University ed., Khon Kaen: 216 pp.

Cottarelli V, Bruno MC, Berera R, 2006. A new species of *Parastenocaris* from Mindoro Island, Philippines: *Parastenocaris distincta* n. sp. (Crustacea: Copepoda: Harpacticoida: Parastenocarididae). Zootaxa 1368:57-68.

Cottarelli V, Bruno MC, Berera R, 2010. First record of Parastenocarididae from Thailand and description of a new genus (Copepoda: Harpacticoida). J. Crustacean Biol. 30: 478-494.

Crandall KA, Buhay JE, 2008. Global diversity of crayfish (Astacidae, Cambaridae, and Parastacidae- Decapoda) in freshwater. Hydrobiologia 595:295-301.

Culver DC, Deharveng L, Bedos A, Lewis JJ, Maden M, Raddell, JR, Sket B, Trontelj P, White DJ, 2006. The mid-latitude biodiversity ridge in terrestrial cave fauna. Ecography 29:120-128.

Day MJ, Urich PB, 2000. An assessment of protected karst landscapes in Southeast Asia. Cave Karst Sci. 27:61-70.

De Grave S, Cai Y, Anker A, 2008. Global diversity of crabs (Crustacea: Decapoda: Caridea) in freshwater. Hydrobiologia 595:287-292.

Deharveng L, 2004. Asia, Southeast: biospeleology, p. 109-112. In: J. Gunn (ed.), Encyclopedia of caves and karst science. Fitzroy Dearborn ed.

Deharveng L, Bedos A, 2000. The cave fauna of Southeast Asia. Origin, evolution and ecology, p. 603-632. In: H. Wilkens, D.C. Culver and W.F. Humphleys (eds.), Ecosystem of the world, 30: subterrnean ecosystems. Elsevier Science.

Deharveng L, Bedos A, 2001. Thailand, p. 1991-2006. In: C. Juberthie and V. Decu (eds.), Encyclopaedia biospeologica, III. Société Internationale de Biospéologie ed.

Deharveng L, Stoch F, Gibert J, Bedos A, Galassi D, Zagmajster M, Brancelj A, Camacho A, Fiers F, Martin P, Giani N, Magniez G, Marmonier P, 2009. Groundwater biodiversity in Europe. Freshwater Biol. 54:709-726.

Dole-Olivier M-J, Catellarini F, Coineau N, Galassi DMP, Martin S, Mori N, Valdecasas A, Gibert J, 2009. Towards an optimal sampling strategy to assess groundwater biodiversity: comparison across six European regions. Freshwater Biol. 54:777-796.

Ellis M, 2006. The caves of Nam Nao National Park, Phetchabun, Thailand. Shepton Mallet Caving Club Publ., Mendips: 1047 pp.

Ellis M, 2012. The distribution and type localities of Thai cave fauna, 3: Isopoda. Available from: http://www.thailandcaves.shepton.org.uk/cave-fauna

Forró L, Korovchinsky NM, Kotov AA, Petrusek A, 2008. Global diversity of cladocerans (Cladocera; Crustacea) in freshwater. Hydrobiologia 595:177-184.

Fosshagen A, Ilife TM, 1989. *Boholina*, a new genus (Copepoda: Calanoida) with two new species from an anchialine cave in the Philippines. Sarsia 74:201-208.

Gibert J, Culver DC, 2009. Assessing and conserving groundwater biodiversity: an introduction. Freshwater Biol. 54:639-648.

Gibert J, Dole-Olivier M-J, Marmonier P, Vervier P, 1990. Surface water-groundwater ecotones, p. 199-225. In: R.J. Naiman and D.H. Camps (eds.), The ecology and management of aquatic-terrestrial ecotones. UNESCO/Parthenon Publ.

Holsinger JR, 1993. Biodiversity of subterranean amphipod crustaceans: global patterns and zoogeographic implications. J. Nat. Hist. 27:821-835.

Hołyńska M, 2000. Revision of the Australasian species of the genus *Mesocyclops* Sars, 1914 (Copepoda: Cyclopidae). Ann. Zool. 50:363-447.

Husana DEM, Naruse T, Kase T, 2009. Two new cavernicolous species of the genus *Sundatephalusa* from Western Samar, Philippines (Decapoda: Brachyura: Parathelphusidae). J. Crustacean Biol. 29:419-427.

Husana DEM, Naruse T, Kase T, 2010. A new species of the genus *Karstarma* (Crustacea: Decapoda: Brachyura: Sesarmidae) from anchialine caves in the Phillippines. Raffles B. Zool. 58:51-55.

Husana DEM, Tan SH, Kase T, 2011. A new genus and species of anchialine Hymenosomatidae (Crustacea, Decapoda, Brachyura) from Samar, Philippines. Zootaxa 3109:49-59.

Jaume D, 2008. Global diversity of spelaeogriphaceans and thermosbaenaceans (Crustacea: Spelaeogriphacea and Thermosbaenacea) in freshwater. Hydrobiologia 595:219-224.

Juberthie C, Decu V, 2001. [Encyclopaedia biospeleologica, III]. [Book in French]. Société Internationale de Biospéologie and Académie Roumaine ed., Moulis and Bucarest: 918 pp.

Kotelatt M, 2004. *Schistura speculi*, a new species of cave fishes from northern Vietnam (Teleostei : Balitoridae). Ichthyol. Explor. Fres. 15:187-191.

Leclerc P, Deharveng L, Ng PKL, Juberthie C, Decu V, 2001. [Indonesie], p. 1805-1823. In: C. Juberthie and V. Decu (eds.), [Encyclopaedia biospeleologica, III]. [Book in French]. Société Internationale de Biospéologie and Académie Roumaine ed.

Lêvêque C, Oberdorff T, Paugy D, Stiassny MLJ, Tedesco PA, 2008. Global diversity of fish (Pisces) in freshwater. Hydrobiologia 595:545-567.

Magniez GJ, Rahmadi C, 2006. A new species of the genus *Stenasellus* (Crustacea, Isopoda, Asellota, Stenasellidae). Bull. Mens. Soc. Linn. L 75:173-177.

Magniez G J, Panitvong N, 2005. A new Stenasellidae from underground waters of Thailand: *Stenasellus mongnatei* sp. nov. (Crustacea, Isopoda, Asellota). Subterr. Biol. 3:69-74.

Martens K, Schön I, Meisch C, Home DJ, 2008. Global diversity of Ostracods (Ostracoda, Crustacea) in freshwater. Hydrobiologia 595:185-193.

Ng PKL, 1991. *Cancrocaeca xenomorpha,* new genus and species, a blind troglobitic freshwater hymenosomatid (Crustacea: Decapoda: Brachyura) from Sulawesi, Indonesia. Raffles B. Zool. 39:59-73.

Ng PKL, Sket B, 1996. The freshwater crab fauna Crustacea: Decapoda: Brachyura) of the Philippies. IV. On a collection of Parathelphusidae from Bohol. P. Biol. Soc. Wash. 109:695-706.

Pesce GL, Argano R, 1981. [Stenasellidi del sud-est Asiatico: *Stenasellus brignolii* n. sp. di Thailandia (Crustacea Isopoda: Asellota)]. [Article in Italian]. Boll. Mus. Civ. Stor. Nat. Verona 8:435-441.

Pesce GL, Apostolov AM, 1985. *Elaphoidella margaritae* sp. n., a new phreatobitic harpacticoid from subterranean waters of Thailand (Crustacea, Copepoda, Canthocamptidae). Acta Zool. Bulgar. 28:70-75.

Price L, 2004. An introduction to some cave fauna of Malaysia and Thailand. Acta Carsol. 31:311-317.

Ranga Reddy Y, Defaye D, 2008. Discovery of the genus *Rybocyclops* Dussart, 1982 (Crustacea, Copepoda, Cyclopoida) in subterranean groundwaters of southeastern India, with description of a new species and its biogeographic significance. Zootaxa 1810:40-50.

Ranga Reddy Y, Drewes J, Schminke HK, 2008. A new species of the genus *Atopobathynella* Schminke, 1973 (Crustacea, Syncarida, Bathynellacea) from the hyporheic zone of the River Godavari, South India. Zootaxa 1829:52-60.

Ranga Reddy Y, Schminke HK, 2009. Co-occurrence of two species of the genus *Habrobathynella* Schminke, 1973 (Crustacea, Malacostraca, Bathynellacea) in sandy sediments of the River Godavari, South India, with the description of a new species. Crustaceana 82:475-485.

Sket B, Fišer C, 2009. A new case of intralacustrine radiation in Amphipoda. A new genus and three new species of Anisogammaridae (Crustaceam, Amphipoda) from the ancient lake Fuxian Hu in Yunan, China. J. Zool. Syst. Evol. Res. 47:115-123.

Stoch F, Galassi DMP, 2010. Stygobiotic crustacean species

richness: a question of numbers, a matter of scale. Hydrobiologia 653:217-234.

Takeda M, Ng PKL, 2001. The Freshwater Crab Fauna (Crustacea, Brachyura) of the Philippines VI. A New Cavernicolous Crab from Mindanao. Zool. Sci. 18:1123-1127.

Tran DL, Chang CY, 2012. Two new species of harpacticoid copepods from anchialine caves in karst area of North Vietnam. Anim. Cells Syst. 16:57-68.

Van Damme K, Brancelj A, Dumont HJ, 2008. Adaptations to the hyporheic in Aloninae (Crustacea: Cladocera): allocation of *Alona protzi* Hartwig, 1900 and related species to *Phreatalona* gen. nov. Hydrobiologia 618:1-34.

Van Damme K, Chiambeng G, Maiphae S, Dumont HJ, 2003. New species in the rheophilous genus *Nicsmirnovius* Chiambeng & Dumont, 1999 (Branchiopoda: Anomopoda: Chydoruidae) and reassignment of *Alona eximia* Kiser, 1948 and *Alona fitzpatricki* Chien, 1970. Hydrobiologia 499:25-49.

Väinölä R, Witt JDS, Grabowski M, Bradbury JH, Jazdzewski K, Sket B, 2008. Global diversity of Amphipods (Amphipoda; Crustacea) in freshwater. Hydrobiologia 595: 241-255.

Vidthayanon C, Kottelat M, 2003. Three new species of fishes from Tham Phra Wang Daeng and Tham Phra Sai Ngam caves in northern Thailand (Teleostei: Cyprinidae and Balitoridae). Ichthyol. Explor. Fres. 14:159-174.

Watiroyram S, 2012. Species diversity and distribution of freshwater Copepoda in caves in northern Thailand. PhD Thesis. Khon Kaen University ed., Khon Kaen: 187 pp.

Watiroyram S, Brancelj A, Sanoamuang L, 2012. A new *Bryocyclops* Kiefer (Crustacea: Copepoda: Cyclopoida) from karstic caves in Thailand. Raffles B. Zool. 60:11-21.

Watiroyram S, Brancelj A, Sanoamuang L (2013). Two new stygobiotic species of *Elaphoidella* (Crustacea: Copepoda: Harpacticoida) with comments on geographical distribution and ecology of harpacticoids from caves in Thailand. Zootaxa (in press).

Weagle JW, Coleman O, Hosse U, 1987. Two new hypogean speciesof *Cynthura* from Melanesia (Crustacea, Isopoda, Anthuridea): further Tethyan relicts? Stygologia 3:89-106.

Wikipedia, 2013. Southeast Asia. Available from: http://en.wikipedia.org/wiki/Southeast_Asia

Wilson GDF, 2008. Global diversity of Isopod Crustaceans (Crustacea; Isopoda) in freshwater. Hydrobiologia 595:231-240.

Yeo DCJ, Ng PKL, Cumberlidge N, Magalhães C, Daniels SR, Campos MR, 2008. Global diversity of crabs (Crustacea: Decapoda: Brachyura) in freshwater. Hydrobiologia 595:275-286.