



Article

Diversity, Distribution, and Habitat Occurrence of the Diaptomid Copepods (Crustacea: Copepoda: Diaptomidae) in Freshwater Ecosystems of Thailand

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Abstract: The diversity, distribution, and checklist of diaptomid copepods from various freshwater ecosystems throughout Thailand are presented, based on data from our biodiversity projects during 1993-2019 and literature reviews. Thailand has one of the most diversified diaptomid fauna in the world, with 42 species identified from 2150 localities (4962 samples). Mongolodiaptomus has the highest species richness with ten species, followed by Tropodiaptomus with seven species. Among these, eight taxa (Arctodiaptomus sp., Mongolodiaptomus pectinidactylus, Neodiaptomus meggitti, Tropodiaptomus hebereri, T. lanaonus, T. oryzanus, T. ruttneri, and Paradiaptomus greeni) are new to the fauna of Thailand. The rare P. greeni, which predominantly occurs in Africa, is also a new record for Southeast Asia. The most frequently encountered species were Mongolodiaptomus botulifer, Phyllodiaptomus praedictus, M. calcarus, M. dumonti, M. malaindosinensis, Vietodiaptomus blachei, Phyllodiaptomus christineae, Eodiaptomus sanoamuangae, Neodiaptomus yangtsekiangensis, E. draconisignivomi, T. vicinus, and Heliodiaptomus elegans. Twelve species appear to be endemic to Thailand, and eight species occur only in the countries belonging to the lower Mekong River Basin (Thailand, Cambodia, Laos, and Vietnam). The uniqueness of the Thai diaptomids is a high degree of co-occurrence of four to seven species in the same localities. Comments on the taxonomic status of the species recorded are provided. In addition, the taxonomic validity of Mongolodiaptomus malaindosinensis is discussed.

Keywords: Arctodiaptomus sp.; biodiversity; Calanoida; lower Mekong River Basin; Mongolodiaptomus malaindosinensis; Paradiaptomus greeni; Southeast Asia

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1. Introduction

Copepods are among the most diverse micro-crustaceans in aquatic habitats [1]. They are abundant in freshwater ecosystems and can be a major component of most planktonic, benthic, and groundwater communities. Members of the family Diaptomidae in the order Calanoida are particularly successful in all kinds of freshwater habitats, comprising over 440 species [2]. Of the 22 genera (92 species) of freshwater diaptomids reported from inland waters of the Oriental biogeographic region, 10 genera (81 species) are endemic to this region [3].

Studies of the freshwater diaptomid copepods in Southeast Asia prior to 1980 were fragmentary. Of the 30 calanoid species, 27 diaptomid species were reported from Southeast Asia [3]. Most of the studies were conducted in Thailand since 1994 [4–22], while a few investigations have been documented in Cambodia [20,21,23], Laos [16,20,24], Malaysia [25–27], Singapore [28], the Philippines [29,30], and Indonesia [31]. A few studies were conducted in Vietnam [20], but most of the publications were published in Vietnamese with an English abstract [32].

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In Thailand, Bricker et al. (1978) reported 7 diaptomid species from 11 reservoirs and one natural swampy lake in Thailand [33]. Later, a list of 14 species based on extensive collections sampled throughout the country was documented by Lai and Fernando (1981) [34]. In 1984, Boonsom (1984) examined samples from 39 different kinds of habitats, including rivers, reservoirs, irrigation tanks, ponds, and fish fields, revealing 8 diaptomid species [35]. In 1994–1998, four new species were described based on specimens from Thailand [4–7]. At the same time, Ranga Reddy et al. (1998) [7] published a list of 17 valid species for the country, and 16 of these were reported from the northeast region by Sanoamuang (1999) [9] as well. The misidentifications and taxonomic confusions of two species (*Neodiaptomus mephistopheles* Brehm, 1933 and *Arctodiaptomus bacillifer* (Koelbel, 1885)) [3,33,34,36] by previous researchers and the doubtful records of two taxa, *Tropodiaptomus doriai* (Richard, 1894) and *Sinodiaptomus chaffanjoni* (Richard, 1897), were corrected by Ranga Reddy et al. (1998) [7].

Consequently, there has been a gradual increase in our knowledge of the diversity of diaptomid copepods in Thailand. Since 2001, 13 more new species have been added to the list of Thailand [10–22]. As part of the authors' long-term intensive collections of freshwater copepods from different habitats all over Thailand during 1993–2019 and from the literature review, an updated list of diaptomid copepods known to date for the country is presented in this contribution. Their distributions within the six regions of Thailand, habitat occurrence, and taxonomic status of the diaptomid taxa are presented here.

2. Materials and Methods

2.1. Study Area

Thailand is situated in the heart of the Southeast Asian mainland, covering an area of 513,115 square kilometers. It lies in the humid tropics, having a monsoon climate with three distinct seasons—hot (March to April), rainy or monsoon (May to October), and cool (November to February). The country is officially divided into six geographical regions (Figure 1A) [36]. The northern region (with 9 provinces) is mountainous and was traditionally the most heavily forested area of the country. There are four main river basins (Ping, Wang, Yom, and Nan) in this region (Figure 1B). The northeast region (with 20 provinces) is some 200-300 m above sea level. This region is hemmed in by mountain ridges on the west and the south. This area is drained by the Song Khram, Chi, and Mun rivers, which are tributaries of the Mekong (Figure 1B). The central region (with 22 provinces) comprises the basins of the Chao Phraya and Pa Sak Rivers, which run from north to south and drain into the Gulf of Thailand. The western region (with 5 provinces) is also mountainous, alternating with plains along narrow valleys. The eastern region (with 7 provinces) is characterized by short mountain ranges and fruit plantations are a major component of agriculture in this area. The southern region (with 14 provinces) has the highest amount of rainfall in the country. It is the principal rubber-growing area and contains extensive alluvial deposits of tin.

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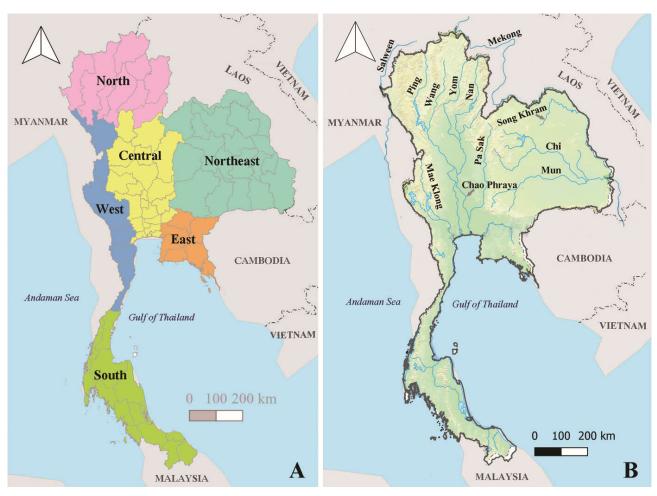


Figure 1. The map of Thailand displays six geographical regions (A) and major rivers (B).

2.2. Sample Collections and Identifications

Qualitative copepod samples of the pelagic and littoral zones from different freshwater habitats in Thailand were collected during 1993–2019. Information on 18 biodiversity projects in the surveyed water bodies is given in Table 1. A total of 4962 samples were collected from 2150 localities in 6 geographical regions (north, northeast, central, east, west, and south) of Thailand using a plankton net with a mesh size of 60 µm. In each site, sampling was performed either in two (dry and rainy) or three (summer, rainy, and winter) seasons, although some were carried out only once. A variety of water bodies, including permanent water habitats—canals, lakes, ponds, swamps, reservoirs, rivers—and temporary water habitats—rice fields, roadside canals, and temporary ponds— were sampled. The animals were preserved on-site in 4% formaldehyde or 70% ethanol. Adult copepods were selected, dissected, and prepared on a glycerin-mounted slide under an Olympus SZ51 stereomicroscope at 40–100-× magnification. All un-dissected specimens were stored in 70% ethanol in 1.5 mL microtubes.

All appendages and body ornamentation were examined at 1000-× magnification under an Olympus CX31 compound microscope. Specimens for scanning electron microscopy (SEM) were dehydrated in an ethanol series (50, 70, 80, 90, 95, 100, and 100%) for 15 min at each concentration. Specimens were dried in a critical-point dryer and were mounted on stubs using adhesive tape under a stereomicroscope. Dried specimens were coated with gold in a sputter coater. The SEM photographs were taken using a scanning electron microscope (LEO, 1450VP).

The abbreviations used in this paper are as follows:

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Exp-2 = second exopodal segment; P5 = leg 5.

Table 1. Information on sampling projects of the surveyed waterbodies in Thailand. The regions in Thailand are given by; N = North, NE = Northeast, C = Central, E = East, W = West, and S = South.

| No. | Sampling Habitats | Regions in Thailand | Sampling Years | Number of Localities | Number of Samples |
|-----|---|------------------------|----------------|-------------------------|----------------------|
| 1 | Various habitats in Northeast Thailand | NE | 1993 | 93 | 200 |
| 2 | Various habitats in Nakhon Ratchasima and Surin Provinces | NE | 1996-1999 | 138 | 412 |
| 3 | Man-made reservoirs in the Phuphan National Park | NE | 1997-1998 | 16 | 336 |
| 4 | Major rivers in Thailand | N,NE,C,E,W,S | 1998-1999 | 20 | 60 |
| 5 | Various habitats throughout Thailand | N,NE,C,E,W,S | 1998-2004 | 294 | 508 |
| 6 | Temporary-water habitats in seven provinces of NE Thailand | NE | 1999-2003 | 521 | 844 |
| 7 | Various habitats in the floodplain of the Rivers Nan, Chi, Mun and Song Khram | N,NE,C | 2000-2004 | 186 | 372 |
| 8 | Various habitats in Central and Northern Thailand | N,C | 2001-2002 | 120 | 360 |
| 9 | Various habitats in Central and Northern Thailand | N,C | 2003 | 55 | 110 |
| 10 | Three natural lakes (Buemg Boraphet, Bueng Khong Long, and Lake Kud- Thing) | NE,C | 2002-2004 | 30 | 60 |
| 11 | Various habitats in Eastern Thailand | Е | 2003-2004 | 55 | 110 |
| 12 | Various habitats in Sisaket Province | NE | 2006-2007 | 99 | 190 |
| 13 | Various habitats in Suphan Buri, Kanchanaburi, Ratchaburi and | W | 2007 | 200 | 218 |

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| | Phetchaburi | | | | |
|----|---------------------|-----|-----------|------|------|
| | Provinces | | | | |
| | Various habitats in | | | | |
| 14 | Nam Nao National | С | 2007-2009 | 10 | 75 |
| 14 | Park, Phetchabun | C | 2007-2007 | 10 | 73 |
| | Province | | | | |
| | Lake Kud-Thing | | | | |
| | and various | | | | |
| 15 | habitats in Bueng | NE | 2012–2014 | 97 | 408 |
| | Kan and Udon | | | | |
| | Thani Provinces | | | | |
| | Various habitats in | | | | |
| 16 | Chiang Rai, Phayao | N | 2014–2016 | 67 | 154 |
| | and Nan Provinces | | | | |
| | Various habitats in | | | | |
| 17 | Khon Kaen, Kalasin | NE | 2014-2018 | 128 | 344 |
| 17 | and Buriram | INL | 2014-2010 | 120 | 311 |
| | Provinces | | | | |
| | Various habitats in | | | | |
| 18 | Saraburi and | C | 2019 | 21 | 201 |
| | Lopburi Provinces | | | | |
| | Total | | | 2150 | 4962 |

2.3. Data Analysis

The relative occurrences of the diaptomid copepods recorded from Thailand are categorized according to the occurrence frequencies of the local populations into five categories as follows: (1) common = species that occurs in more than 45% of the sampled localities; (2) fairly common = species that occurs in 31–45% of the sampled localities; (3) uncommon = species that occurs in 16–30% of the sampled localities; (4) rare = species that occurs in 5–15% of the sampled localities; (5) extremely rare = species that occurs in less than 5% of the sampled localities.

3. Results

3.1. Species Diversity

A list of diaptomid species identified from the samples examined, along with their habitat types, relative occurrences, and distributional regions in Thailand, is provided in Table 2. Of the 42 species identified, 41 species are members of the subfamily Diaptominae, while only 1 belongs to the subfamily Paradiaptominae. The diversity of species among the 11 genera of the Diaptomidae is dominated by the genus Mongolodiaptomus, with 10 known species, followed by Tropodiaptomus (7 species), Neodiaptomus (6 species) and Phyllodiaptomus (6 species). Among these, 17 species (40.5% of the species recorded) have been originally described from specimens from Thailand since 1994, including (1) Phyllodiaptomus (Ctenodiaptomus) praedictus Dumont and Ranga Reddy, 1994 (Figure 2A); (2) Phyllodiaptomus (Phyllodiaptomus) christineae Dumont, Ranga Reddy, and Sanoamuang, 1996 (Figure 2B); (3) Eodiaptomus sanoamuangae Ranga Reddy and Dumont, 1998 (Figure 3A); (4) Mongolodiaptomus rarus (Ranga Reddy, Sanoamuang, and Dumont, 1998); (5) Phyllodiaptomus (Ctenodiaptomus) surinensis Sanoamuang and Yindee, 2001; (6) Eodiaptomus phuphanensis Sanoamuang, 2001 (Figure 3B); (7) Mongolodiaptomus dumonti Sanoamuang, 2001 (Figure 4A); (8) Neodiaptomus songkhramensis Sanoamuang and Athibai, 2002; (9) Heliodiaptomus phuthaiorum Sanoamuang, 2004 (Figure 5A); (10) Eodiaptomus Water **2021**, 13, 2381 6 of 30

phuvongi Sanoamuang and Sivongxay, 2005 (Figure 3C); (11) Phyllodiaptomus (Phyllodiaptomus) thailandicus Sanoamuang and Teeramaethee, 2006 (Figure 2C); (12) Neodiaptomus siamensis Proogkiat and Sanoamuang, 2008; (13) Mongolodiaptomus loeiensis Watiroyram and Sanoamuang, 2017 (Figure 4B); (14) Mongolodiaptomus mekongensis Sanoamuang and Watiroyram, 2018 (Figure 4C); (15) Phyllodiaptomus (Phyllodiaptomus) roietensis (Sanoamuang and Watiroyram, 2020) (Figure 2D); (16) Tropodiaptomus megahyaline Saetang, Sanoamuang, and Maiphae, 2020; (17) Dentodiaptomus orientalis Sanoamuang and Watiroyram, 2021. In addition to the above, four more undescribed species (Arctodiaptomus sp., Mongolodiaptomus sp., Phyllodiaptomus sp. and Tropodiaptomus sp.) are waiting to be described.

Eight taxa—namely, *Arctodiaptomus* sp. (Figure 5B), *Mongolodiaptomus pectinidactylus* (Shen and Tai, 1964) (Figure 4D), *Neodiaptomus meggitti* Kiefer, 1932, *Tropodiaptomus hebereri* (Kiefer, 1930) (Figure 6A), *T. lanaonus* Kiefer, 1982, *T. oryzanus* Kiefer, 1937 (Figure 6B,C), *T. ruttneri* (Brehm, 1923) (Figure 6D), and *Paradiaptomus greeni* (Gurney, 1906) (Figure 5C,D)—are new to the fauna of Thailand. Moreover, this is the first record of a species complex of *P. greeni* in the subfamily Paradiaptominae in Southeast Asia.

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Table 2. A list of the diaptomid copepods recorded with their habitat types, distributional regions, and relative occurrences in the freshwater ecosystems of Thailand. C = canal, L = lake, Pp/Sw = permanent pond/swamp, Re = reservoir, Ri = river, Rf = rice field, Rc = roadside canal, and Tp = temporary pond/rain pool. The distributional regions of Thailand are given by; N = North, NE = Northeast, C = Central, E = East, W = West, and S = South. Species with bold letters and marked with * are new records for Thailand.

| | | | |] | Habita | t Type | s | | | | Dist | ributio | nal Re | gions | | |
|----|---|--------|-------|-----------|--------|--------|----|------------------|----|---|------|---------|--------|-------|---|-------------------|
| No | Species | | Pern | nanent w | vaters | | | empora waters | | | | | | | | Relative |
| | | С | L | Pp/S w | Re | Ri | Rf | Rc | Тр | N | NE | С | E | w | S | - Occurrences |
| | Subfamily | Diapto | minae | Kiefer, | 1932 | | | | | | | | | | | |
| 1 | Allodiaptomus raoi Kiefer, 1936 | | ✓ | | ✓ | ✓ | ✓ | | | | ✓ | | | | | uncommon |
| 2 | Arctodiaptomus sp. | | | | | ✓ | | | | | ✓ | | | | | extremely rare |
| 3 | Dentodiaptomus javanus (Grochmalicki, 1915) | | | ✓ | | | ✓ | ✓ | ✓ | ✓ | ✓ | | ✓ | ✓ | | fairly common |
| 4 | Dentodiaptomus orientalis Sanoamuang & Watiroyram, 2021 | | | ✓ | | | | ✓ | ✓ | | ✓ | | | | | uncommon |
| 5 | Eodiaptomus draconisignivomi Brehm, 1952 | ✓ | ✓ | ✓ | ✓ | ✓ | | | | | ✓ | ✓ | ✓ | ✓ | | fairly common |
| 6 | Eodiaptomus phuphanensis Sanoamuang, 2001 | | | | ✓ | ✓ | | ✓ | ✓ | | ✓ | | | ✓ | | fairly common |
| 7 | Eodiaptomus phuvongi Sanoamuang & Sivongxay, 2004 | ✓ | | ✓ | | | | | ✓ | | ✓ | | | | | fairly common |
| 8 | Eodiaptomus sanoamuangae Ranga Reddy & Dumont, 1998 | ✓ | ✓ | ✓ | ✓ | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | | ✓ | | common |
| 9 | Heliodiaptomus elegans Kiefer, 1935 | | ✓ | ✓ | ✓ | ✓ | | | ✓ | ✓ | ✓ | | | ✓ | | fairly common |
| 10 | Heliodiaptomus phuthaiorum Sanoamuang, 2004 | | | | | | | ✓ | ✓ | | ✓ | | | | | rare |

| 11 | Heliodiaptomus viduus (Gurney, 1916) | ✓ | ✓ | ✓ | ✓ | | | | | ✓ | | ✓ | ✓ | ✓ | | uncommon |
|----|---|---|---|---|---|---|---|---|---|---|----------|---|---|---|---|-------------------|
| 12 | Mongolodiaptomus botulifer (Kiefer, 1974) | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | common |
| 13 | Mongolodiaptomus calcarus (Shen & Tai, 1965) | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | | ✓ | ✓ | common |
| 14 | Mongolodiaptomus dumonti Sanoamuang, 2001 | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | | common |
| 15 | Mongolodiaptomus loeiensis Watiroyram & Sanoamuang, 2017 | | | | | | | | ✓ | | √ | | | | | extremely rare |
| 16 | Mongolodiaptomus malaindosinensis (Lai & Fernando, 1978) | | ✓ | ✓ | ✓ | ✓ | | | ✓ | ✓ | ✓ | ✓ | ✓ | | ✓ | common |
| 17 | Mongolodiaptomus mekongensis Sanoamuang & Watiroyram, 2018 | | | ✓ | | | ✓ | ✓ | ✓ | | ✓ | | | | | uncommon |
| 18 | Mongolodiaptomus pectinidactylus (Shen & Tai, 1964) * | | ✓ | | | | | | ✓ | | ✓ | | | | | rare |
| 19 | Mongolodiaptomus rarus (Ranga Reddy, Sanoamuang & Dumont, 1998) | | | | | | ✓ | ✓ | ✓ | | ✓ | | | | | uncommon |
| 20 | Mongolodiaptomus uenoi (Kikuchi, 1936) | ✓ | | ✓ | ✓ | ✓ | | ✓ | ✓ | | ✓ | | | | | fairly common |
| 21 | Mongolodiaptomus sp. | | | ✓ | | | | | ✓ | | ✓ | | | | | extremely rare |
| 22 | Neodiaptomus laii Kiefer, 1974 | ✓ | | ✓ | | | | | ✓ | | ✓ | | ✓ | | ✓ | uncommon |
| 23 | Neodiaptomus meggitti Kiefer, 1932 * | | | ✓ | | | | | | ✓ | | | - | | | extremely rare |

| 24 | Neodiaptomus schmackeri (Poppe & Richard, 1892) | ✓ | | ✓ | | | ✓ | ✓ | ✓ | ✓ | | ✓ | | ✓ | | fairly common |
|----|--|---|---|---|---|---|---|---|---|---|---|---|---|---|---|-------------------|
| 25 | Neodiaptomus siamensis Proogkiat & Sanoamuang, 2008 | | | | | | | | ✓ | | | ✓ | | | | extremely rare |
| 26 | Neodiaptomus songkhramensis Sanoamuang & Athibai, 2002 | | | | | | ✓ | ✓ | ✓ | | ✓ | | | | | uncommon |
| 27 | Neodiaptomus yangtsekiangensis Mashiko, 1951 | ✓ | ✓ | ✓ | ✓ | ✓ | | ✓ | ✓ | | ✓ | | ✓ | | ✓ | common |
| 28 | Phyllodiaptomus (Ctenodiaptomus) praedictus Dumont & Ranga Reddy, 1994 | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | | common |
| 29 | Phyllodiaptomus (Ctenodiaptomus) surinensis Sanoamuang & Yindee, 2001 | ✓ | | | | | | | | | ✓ | | | | | extremely rare |
| 30 | Phyllodiaptomus (Phyllodiaptomus) christineae Dumont, Ranga Reddy & Sanoamuang, 1996 | ✓ | ✓ | ✓ | ✓ | ✓ | | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | | common |
| 31 | Phyllodiaptomus (Phyllodiaptomus) roietensis Sanoamuang & Watiroyram, 2020 | | | | | | ✓ | ✓ | ✓ | | ✓ | | | | | rare |
| 32 | Phyllodiaptomus (Phyllodiaptomus) thailandicus Sanoamuang & Teeramaethee, 2006 | ✓ | | ✓ | | | | | ✓ | | | | ✓ | ✓ | ✓ | rare |
| 33 | Phyllodiaptomus (Phyllodiaptomus) sp. | | | ✓ | | | | | ✓ | | ✓ | | | | | rare |
| 34 | Tropodiaptomus hebereri (Kiefer, 1930) * | ✓ | | | | | | | | ✓ | | | | | | extremely rare |
| 35 | Tropodiaptomus lanaonus Kiefer, 1982 * | | ✓ | | | | | | | | ✓ | ✓ | | | | rare |

| 36 | Saetang, Sanoamuang & | | ✓ | ✓ | | | ✓ | | | | ✓ | | | | | rare |
|----|--|--------|--------|---------|----------|---|---|---|---|----|----|----|----|----|---|-------------------|
| 37 | Maiphae, 2020 Tropodiaptomus oryzanus Kiefer, 1937 * | | ✓ | | | | ✓ | ✓ | ✓ | | ✓ | | | | | uncommon |
| 38 | Tropodiaptomus ruttneri (Brehm, 1923) * | | | | | | ✓ | | ✓ | ✓ | ✓ | | | | | uncommon |
| 39 | Tropodiaptomus vicinus (Kiefer, 1930) | ✓ | ✓ | ✓ | | ✓ | | | | ✓ | ✓ | ✓ | | ✓ | ✓ | fairly common |
| 40 | Tropodiaptomus sp. | | | | | | | | ✓ | ✓ | | | | | | extremely rare |
| 41 | Vietodiaptomus blachei (Brehm, 1951) | ✓ | ✓ | ✓ | ✓ | | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | | ✓ | ✓ | common |
| | Subfamily Pa | radiap | tomina | e Kiefe | er, 1932 | | | | | | | | | | | |
| 42 | Paradiaptomus greeni (Gurney, 1906) * | | | | | | | | ✓ | | ✓ | | | | | extremely rare |
| | | | Total | | | | | | | 17 | 35 | 14 | 11 | 15 | 8 | |

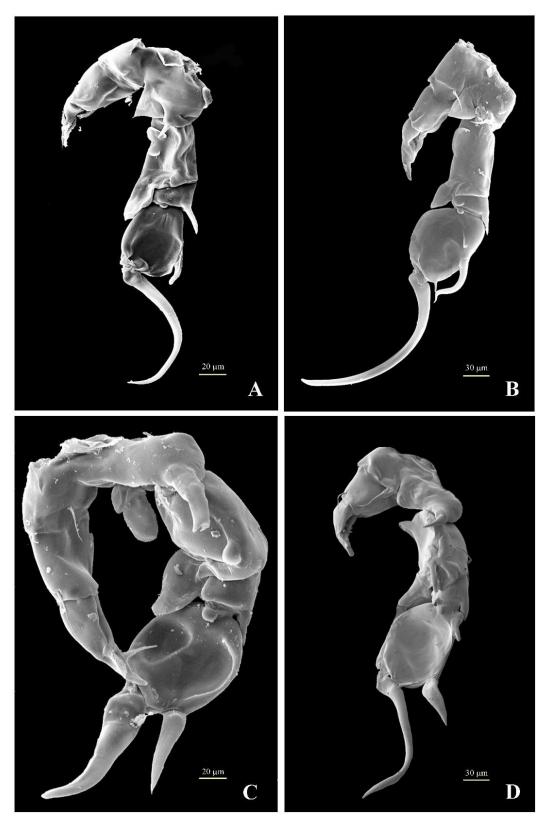


Figure 2. SEM photographs of the male leg 5 (P5) of four species of the genus *Phyllodiaptomus*: (**A**) *P.* (*C.*) *praedictus*; (**B**). *P.* (*P.*) *christineae*; (**C**). *P.* (*P.*) *thailandicus*; and (**D**). *P.* (*P.*) *roietensis*.

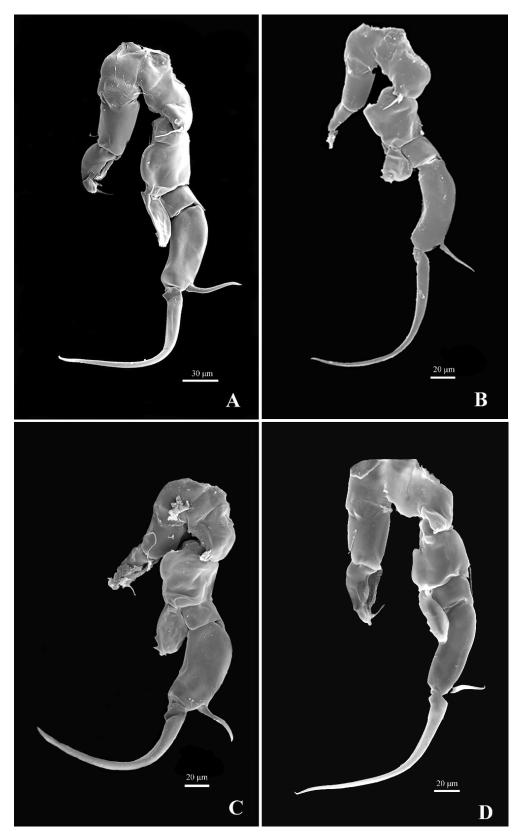


Figure 3. SEM photographs of the male leg 5 (P5) of four species of the genus Eodiaptomus: (**A**) *E. sanoamuangae*; (**B**) *E. Phuphanensis*; (**C**) *E. phuvongi*; and (**D**) *E. draconisignivomi*.

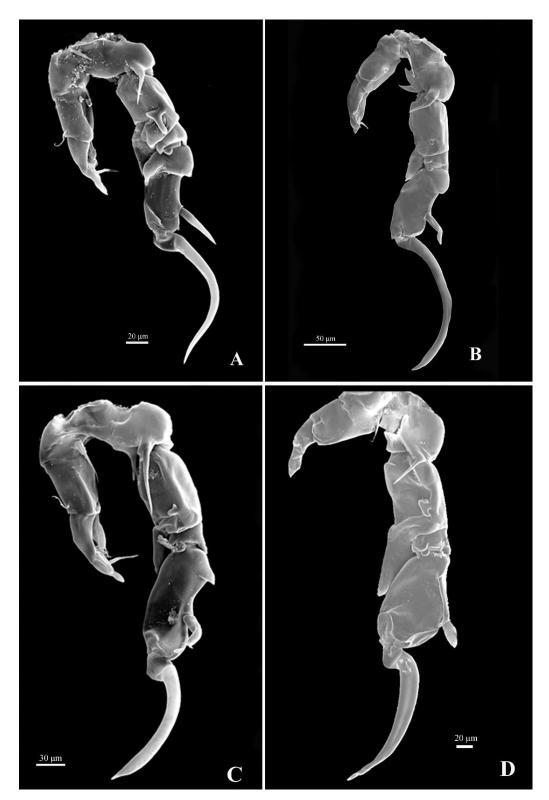


Figure 4. SEM photographs of the male leg 5 (P5) of four species of the genus Mongolodiaptomus: (**A**) M. dumonti; (**B**) M. loeiensis; (**C**) M. mekongensis; and (**D**) M. pectinidactylus.

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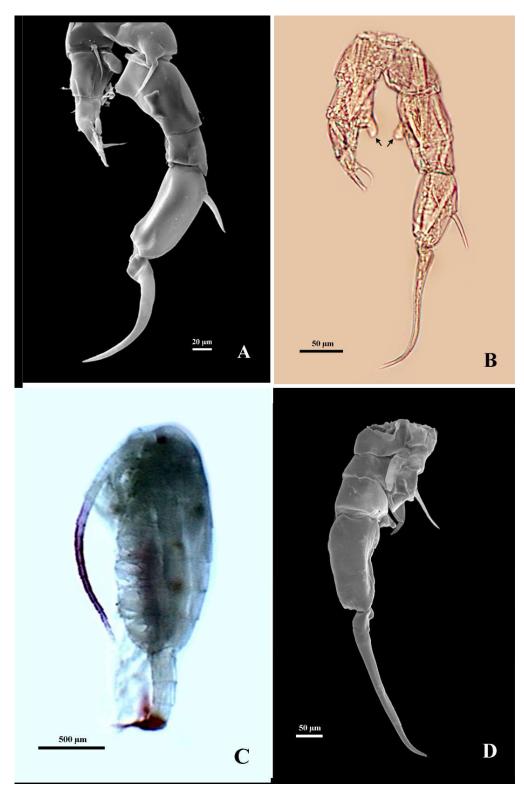


Figure 5. Photographs of three species of diaptomid copepods. (**A**) male P5 of *Heliodiaptomus phuthaiorum*; (**B**) male P5 of *Arctodiaptomus* sp. (black arrows point to left and right hyaline membranes on left and right bases; (**C**) habitus of male *Paradiaptomus greeni*; (**D**) male P5 of *P. greeni*.

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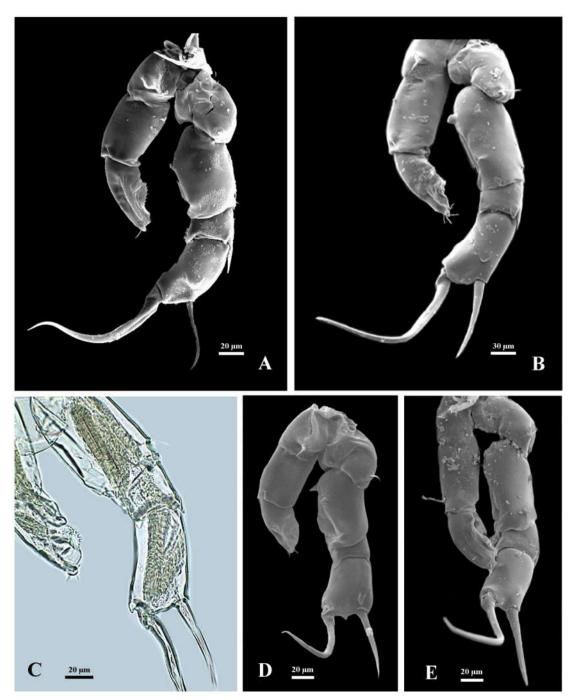


Figure 6. Photographs of the male leg 5 (P5) of four species of the genus *Tropodiaptomus*: (**A**) *T. hebereri*; (**B**) *T. oryzanus*; (**C**) *T. oryzanus*, showing detail of left P5; and (**D**) *T. ruttneri*; (**E**) *T. vicinus*.

3.2. Relative Occurrences and Distribution

Twelve species (28.6%) are commonly found in different kinds of habitats, and most are widely distributed throughout the six regions of Thailand. The most frequently encountered species in the sampled localities were *Mongolodiaptomus botulifer* (Figure 7A), *Phyllodiaptomus praedictus* (Figure 2A), *M. calcarus* (Figure 7B), *M. dumonti* (Figure 4A), *M. malaindosinensis* (Figure 7C), *Vietodiaptomus blachei* (Figure 8A), *P. christineae* (Figure 2B), *Eodiaptomus sanoamuangae* (Figure 3A), *Neodiaptomus yangtsekiangensis*, *E. draconisignivomi* (Figure 3D), *T. vicinus* (Figure 6E), and *H. elegans* (Figure 8B). The rest, including five fairly

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common, nine uncommon, seven rare, and nine extremely rare species, are also listed in Table 2.



Figure 7. SEM photographs of the male leg 5 (P5) of four species of the genus *Mongolodiaptomus*: (**A**) *M. botulifer*; (**B**) *M. calcarus*; (**C**) *M. malaindosinensis*; and (**D**) *M. uenoi*.

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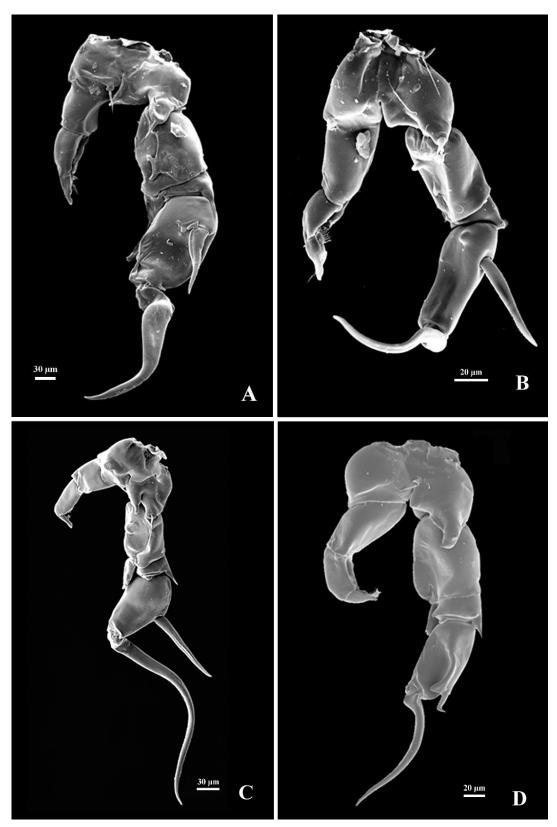


Figure 8. SEM photographs of the male leg 5 (P5) of four species of the diaptomid copepods: **(A)** *Vietodiaptomus blachei*; **(B)** *Heliodiaptomus elegans*; **(C)** *Neodiaptomus schmackeri*; and **(D)** *Dentodiaptomus javanus*.

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The species richness of the diaptomids ranged from 1 to 7 species per locality at the same sampling dates. Although 2–3 species usually coexist in the same location, the coexistence of 4–7 diaptomid species has been observed in northeastern Thailand, particularly in temporary water habitats (Table 3). The co-occurrence of congeneric species was about 50% of the localities having co-occurrence records, and it was predominantly found in small water bodies. *M. botulifer* showed the highest co-occurrences with other species, followed by *M. dumonti*, *M. malaindosinensis*, *P. (P.) christineae*, and *V. blachei*.

It is noted that eight species (*Heliodiaptomus phuthaiorum* (Figure 5A), *Mongolodiaptomus loeiensis* (Figure 4B), *M. rarus, Neodiaptomus siamensis, N. songkhramensis, Phyllodiaptomus roietensis* (Figure 2D), *Tropodiaptomus* sp. and *Paradiaptomus greeni* (Figure 5C,D)) appear to occur only in temporary waters. The northeast is the most diverse region, with 35 recorded species. The other regions have 8–17 species.

Table 3. Co-occurrences of up to 7 species of diaptomid copepods in freshwater habitats in Northeast Thailand.

| Localities | Sampling Dates | Co-occurrence of Diaptomid Species |
|--|-----------------|--------------------------------------|
| | | 1. Dentodiaptomus javanus |
| | | 2. Mongolodiaptomus dumonti |
| Canal at Ban Paiklao, Chumphon Buri | 2 April 1999 | 3. Mongolodiaptomus malaindosinensis |
| District, Surin Province | 2 April 1999 | 4. Mongolodiaptomus uenoi |
| | | 5. Neodiaptomus yangtsekiangensis |
| | | 6. Phyllodiaptomus (P.) christineae |
| | | 1. Dentodiaptomus javanus |
| | | 2. Mongolodiaptomus dumonti |
| I | | 3. Neodiaptomus laii |
| Irrigation Canal at Ban Nayom, Sanom District, Surin Province | 29 July 1999 | 4. Phyllodiaptomus (P.) christineae |
| District, Surin Frovince | | 5. Phyllodiaptomus (C.) surinensis |
| | | 6. Tropodiaptomus oryzanus |
| | | 7. Tropodiaptomus vicinus |
| | | 1. Dentodiaptomus javanus |
| T I I D CI I D I | | 2. Eodiaptomus phuphanensis |
| Temporary pond at Ban Chaiya Buri, | 10 M 2000 | 3. Heliodiaptomus phuthaiorum |
| Chaiya Buri Sub-district, Tha Uthen | 18 May 2000 | 4. Mongolodiaptomus malaindosinensis |
| District, Nakhon Phanom Province | | 5. Neodiaptomus yangtsekiangensis |
| | | 6. Vietodiaptomus blachei |
| | | 1. Eodiaptomus phuphanensis |
| Roadside canal (temporary-water | | 2. Mongolodiaptomus pectinidactylus |
| habitat), KM 24, Road #2050, Lao | 0 1 2002 | 3. Mongolodiaptomus uenoi |
| Suekok Sub-district, Ubon Rachathani | 8 June 2002 | 4. Neodiaptomus yangtsekiangensis |
| Province | | 5. Tropodiaptomus oryzanus, |
| | | 6. Vietodiaptomus blachei |
| | | 1. Allodiaptomus raoi |
| Lake Bueng Khong Long, Bueng | | 2. Heliodiaptomus elegans |
| Khong Long District, Bueng Kan | 13 August 2002 | 3. Mongolodiaptomus pectinidactylus |
| Province | | 4. Neodiaptomus yangtsekiangensis |
| | | 5. Tropodiaptomus megahyaline |
| Roadside canal (temporary-water | | 1. Eodiaptomus phuphanensis |
| habitat), Ban Dirkai, Muangsamsip | 19 October 2002 | 2. Heliodiaptomus elegans |
| District, Ubon Rachathani Province | | 3. Mongolodiaptomus malaindosinensis |

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| | | 4. Neodiaptomus yangtsekiangensis 5. Phyllodiaptomus (P.) christineae |
|------------------------------------|-------------|--|
| | | 5. Pnyttoutaptomus (P.) christineue 6. Vietodiaptomus blachei |
| | | 1. Eodiaptomus phuphanensis |
| | | 2. Mongolodiaptomus malaindosinensis |
| Temporary pond at Ban Thasongcorn, | | 3. Mongolodiaptomus uenoi |
| Panna Nikom District, Sakon Nakhon | 17 May 2004 | 4. Neoodiaptomus songkhramensis |
| Province | | 5. Neodiaptomus yangtsekiangensis |
| | | 6. Tropodiaptomus oryzanus, |
| | | 7. Vietodiaptomus blachei |

The species recorded from Thailand can be classified according to their zoo-geographical distribution into six groups. The list of species endemic to Thailand, the lower Mekong River Basin, and Southeast Asia is provided in Table 4. Overall, 12 (28.6%) of the species recorded appear to be endemic to Thailand. Eight species (19%) have a more restricted distribution, occurring in the lower Mekong River Basin (Thailand, Laos, Cambo-dia, and Vietnam), while the other eight species are widely distributed in the countries in the lower Mekong River Basin plus the other Southeast Asian countries, including Malay-sia, Singapore, Indonesia, and the Philippines (Table 4). In addition, 10 species (23.8%) are widely distributed in Southeast Asia and East Asia. Three species—Heliodiaptomus elegans (Figure 8B), Heliodiaptomus viduus, and Neodiaptomus schmackeri (Figure 8C)—are the most widely distributed across Southeast, East, and South Asia. Another species with a wide distribution is Paradiaptomus greeni (Figure 5C,D), occurring in Southeast Asia, South Asia, and Africa.

Table 4. Diaptomid copepods from Thailand are classified according to their general geographic distribution. The Lower Mekong River Basin region consists of Thailand, Myanmar, Laos, Cambodia, and Vietnam. The Southeast Asian region consists of Thailand, Myanmar, Laos, Cambodia, Vietnam, Malaysia, Singapore, the Philippines, Indonesia, and Brunei. The East Asian region consists of China, Japan, North Korea, South Korea, Mongolia, and Taiwan. The South Asian region consists of India, Sri Lanka, Afghanistan, Bangladesh, Bhutan, Nepal, and Pakistan.

| Distributional Regions | Number of Species | % of Species Recorded | List of Species |
|---------------------------------|-------------------|--------------------------|---------------------------------------|
| | | | Arctodiaptomus sp., |
| | | | Heliodiaptomus phuthaiorum, |
| | | | Mongolodiaptomus dumonti, |
| | | | M. loeiensis, M. rarus, |
| Theiland only | | | Mongolodiaptomus sp. |
| Thailand only (Endemic species) | 12 | 28.6 | Neodiaptomus siamensis, N. |
| (Endenne species) | | | songkhramensis, |
| | | | Phyllodiaptomus (C.) surinensis, |
| | | | P. (P.) thailandicus, |
| | | | Tropodiaptomus megahyaline, |
| | | | Tropodiaptomus. sp. |
| | | | Dentodiaptomus orientalis, |
| | | | Eodiaptomus draconisignivomi, |
| | | | E. phuphanensis, E. phuvongi, |
| Lower Mekong River Basin | 8 | 19.0 | Mongolodiaptomus |
| | | | mekongensis, Phyllodiaptomus |
| | | | (P.) christineae, P. (P.) roietensis, |
| | | | Phyllodiaptomus sp. |

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| Southeast Asia | 8 | 19.0 | Mongolodiaptomus botulifer, M. malaindosinensis, Neodiaptomus laii, N. meggitti, Phyllodiaptomus (C.) praedictus, Tropodiaptomus lanaonus, T. vicinus, Vietodiaptomus blachei |
|---|----|------|--|
| Southeast Asia and East Asia | 10 | 23.8 | Allodiaptomus raoi, Dentodiaptomus javanus, Eodiaptomus sanoamuangae, Mongolodiaptomus calcarus, M. pectinidactylus, M. uenoi, Neodiaptomus yangtsekiangensis, Tropodiaptomus hebereri, T. oryzanus, T. ruttneri |
| Southeast Asia, East Asia and South Asia | 3 | 7.2 | Heliodiaptomus elegans, Heliodiaptomus viduus, Neodiaptomus schmackeri |
| Southeast Asia, South Asia and Africa | 1 | 2.4 | Paradiaptomus greeni |
| Total | 42 | 100 | |

3.3. Taxonomic Checklist

Comments on the relative occurrences, distributional information, and taxonomic status of the species recorded in the present study are provided alphabetically according to the genera. In addition, information on the geographical distribution of the species in other countries, particularly Southeast Asian countries, is documented here. Order Calanoida Sars, 1903; Family Diaptomidae Baird, 1850; Subfamily Diaptominae Kiefer, 1932.

3.3.1. Genus Allodiaptomus Kiefer, 1936

Allodiaptomus raoi Kiefer, 1936 is an uncommon species that occurrs in lakes, reservoirs, rivers, and rice fields in the northeast of Thailand. It was originally described in south India [37] and has been found in Cambodia [23], Vietnam [32], and China [38].

3.3.2. Genus Arctodiaptomus Kiefer, 1932

Arctodiaptomus sp. (Figure 5B) is identified as an undescribed species based on specimens collected from the Mun River, Ubon Ratchathani Province, northeastern Thailand. Since only one male specimen was collected, the description of this species will be provided when more specimens are available. According to the typical pincer-like processes at the end of the exopod of the male left P5 and a distinct hyaline membrane on the inner margin of the basis of both the left and right P5s in the male (Figure 5B), this species is placed in the genus Arctodiaptomus. The record of this genus in Thailand is unexpected since members of this genus inhabit water bodies across Eurasia, North Africa, and North Asia, including China [38]. In Southeast Asia, only Arctodiaptomus dorsalis (Marsh, 1907) has been recorded in more than 20 lakes in the Philippines [39]. This Neotropical species was originally described from the United States and has been found across Central America to northern South America [40]. A. dorsalis has been introduced to the Philippines since 1991 [41]. This species has been documented to prefer eutrophic conditions. Most native calanoids may have been displaced by this invasive species.

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3.3.3. Genus Dentodiaptomus Shen and Tai, 1964

Dentodiaptomus javanus (Grochmalicki, 1915) (Figure 8D) was originally described from Java (Indonesia) as Diaptomus javanus [42]. In 1964, this taxon was raised as a type species of the genus Dentodiaptomus by Shen and Tai (1964) [43]. The presence of at least one "denticle" or "tooth-like process" on the male left P5 Exp-2 is a unique character that was used to name the genus Dentodiaptomus [43]. Another distinct characteristic of the male right P5 of this genus is the Exp-2, a longitudinal ridge on the posterior surface that terminates near the insertion of the principal spine. This ridge is not observed in other genera of diaptomids. In Thailand, this species commonly occurs in every type of temporary habitat (rice fields, roadside canals, temporary ponds) [9] and permanent ponds or swamps. It is widely distributed in the northeastern region but sporadic in the northern, eastern, and western regions. D. javanus has been found in Cambodia [23], Indonesia [31], Vietnam [32], and southern China [38].

Dentodiaptomus orientalis Sanoamuang and Watiroyram, 2021 is a newly described taxon, recorded from five and six localities in the floodplain of the lower Mekong River Basin in Thailand and Cambodia, respectively [44]. D. orientalis is an uncommon taxon and has been found only in the northeast of Thailand in both temporary and permanent water habitats throughout the year. The new species differs from its congener in many morphological aspects, especially on their fifth legs. The male left P5 Exp-2 of this species has three inner distal denticles instead of one as in D. javanus.

3.3.4. Genus Eodiaptomus Kiefer, 1932

Eodiaptomus draconisignivomi Brehm, 1952 (Figure 3D) was described from the neighborhood of the Mekong River, Cambodia, in 1952 [45]. In Thailand, it is a common species occurring in permanent water bodies such as canals, rivers, lakes, reservoirs, and swamps in the northeastern, central, eastern, and western parts of the country [10]. This species appears to be a widely distributed diaptomid in the lower Mekong River Basin, as it is known from Cambodia [46], Laos [47], and Vietnam [32].

Eodiaptomus phuphanensis Sanoamuang, 2001 (Figure 3B) is a fairly common species inhabiting both permanent and temporary habitats but has been so far reported only in the northeast [11] and western Thailand (this study). It was first collected from two reservoirs in the Phu Phan National Park in 2001 [11]. This species has been recorded in Cambodia and central Laos [47].

Eodiaptomus phuvongi Sanoamuang and Sivongxay, 2004 (Figure 3C) was described based on specimens collected from Thailand and Laos [16]. It is a fairly common species, especially in temporary habitats in northeastern Thailand, and is also found in canals, permanent ponds, and swamps. This species is morphologically most similar to E. phuphanensis by having a characteristically flat endopod on the male right P5. However, they can be distinguished from each other in the following features of the male P5: (1) the hyaline lamella on the inner margin of the right basis of E. phuvongi is semicircular, but it is rectangular in E. phuphanensis, and (2) the basis of the left P5 has a distinct spiny knob in E. phuvongi but lacks this knob in E. phuphanensis.

Eodiaptomus sanoamuangae Ranga Reddy and Dumont, 1998 (Figure 3A) was first collected from a roadside canal in Khon Kaen Province, northeastern Thailand [6]. It is a common species and has been found in every type of both permanent and temporary water bodies, except rivers [10]. This taxon was previously confused with the Chinese E. sinensis (Burckhardt, 1913) by Mashiko (1951) [48]. To date, E. sanoamuangae is known in the north, northeast, and west of Thailand (this study), and in the Yangtze River, and its tributaries in central China [48].

3.3.5. Genus Heliodiaptomus Kiefer, 1932

Heliodiaptomus elegans Kiefer, 1935 (Figure 8B) was briefly described based on specimens from Myanmar [49] and was redescribed from samples collected from Thailand by

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Ranga Reddy and Dumont (1999) [50]. It is a common species and has been found mostly in permanent water bodies, but sometimes in temporary ponds in the north, northeast, and west of Thailand. It has been reported from Cambodia [23], Bangladesh [50], Vietnam [32], and China [38].

Heliodiaptomus phuthaiorum Sanoamuang, 2004 (Figure 5A) was described from 9 of the 456 sampled localities in northeastern Thailand [13]. This species is rare and has been found only in temporary waters, such as ponds and roadside canals, in the vicinity of the Song Khram River, a tributary of the Mekong River.

Heliodiaptomus viduus (Gurney, 1916) is an uncommon species and has been recorded only in permanent water bodies (canals, lakes, swamps, ponds, and reservoirs) in the north, central, east, and west of Thailand ([9], this study). It was first described as Diaptomus viduus from Sri Lanka [51] and has been found in Myanmar and Pakistan. This species is a common diaptomid in southern India and Bangladesh [52].

3.3.6. Genus Mongolodiaptomus Kiefer, 1937

A criterion relating to the armature details of the second exopodal segment of the male right P5 has been proposed to differentiate the genus *Mongolodiaptomus* from the close congeners *Neodiaptomus* and *Allodiaptomus* by Ranga Reddy et al. (2000) [8]. Thus, some species of both genera have been transferred to *Mongolodiaptomus*.

Mongolodiaptomus botulifer (Kiefer, 1974) (Figure 7A) was originally described as Neodiaptomus botulifer from Malaysia [53] and redescribed using specimens from Thailand by Ranga Reddy et al. (1998) [7]. It is the most common diaptomid copepod and always occurs in great abundance in Thailand. This species inhabits every type of freshwater habitat in every region of the country. M. botulifer has also been reported in Singapore [28], Cambodia [3], Vietnam [32], and Laos [47].

Mongolodiaptomus calcarus (Shen and Tai, 1965) (Figure 7B) was originally described as Allodiaptomus calcarus from China [54] and redescribed by Ranga Reddy et al. (1998) [7]. Specimens of this species from Malaysia, Singapore, and Thailand have been confused with the Javan Neodiaptomus mephistopheles Brehm, 1933 by Lai and Fernando (1981, 1978) [34,55] and Schmoker et al. (2014) [28]. According to Ranga Reddy et al. (1998) [7], it is in fact M. calcarus, not N. mephistopheles. It is one of the most common diaptomids in Thailand, occurring in every type of freshwater habitat in the north, northeast, central, west, and south of Thailand. M. calcarus has also been found in western Java, Indonesia, Laos [47], and Vietnam [32].

Mongolodiaptomus dumonti Sanoamuang, 2001 (Figure 4A) was discovered in a reservoir and several localities in northeastern Thailand and then described by Sanoamuang (2001) [12]. It is a common freshwater calanoid occurring in every type of freshwater habitat in the north, northeast, central, east, and west of Thailand.

Mongolodiaptomus loeiensis Watiroyram and Sanoamuang, 2017 (Figure 4B) was collected from a temporary pond in Loei Province of northeastern Thailand and described by Watiroyram and Sanoamuang (2017) [19]. It is an extremely rare taxon and has to date been found only in the type locality. This species was the single calanoid found in the type locality. M. loeiensis appears to be an endemic diaptomid of Thailand.

Mongolodiaptomus malaindosinensis (Lai and Fernando, 1978) (Figure 7C) was originally described as Neodiaptomus malaindosinensis based on specimens from Malaysia [56]. However, Ranga Reddy et al. (1998) [7] observed some morphological variabilities in M. botulifer from Thailand, leading to serious doubt about the validity of the closely allied M. malaindosinensis. Although the morphological features of the two congeners are similar, they can be distinguished from each other by the following characters: (1) male right P5 basis with a large, spherical hyaline lamella on the inner margin in M. botulifer (Figure 7A) versus a triangular hyaline lamella in M. malaindosinensis (Figure 7C); (2) male right P5 Exp-2 with a blunt chitinous process on the outer proximal third margin in M. botulifer versus minute 1–4 hyaline knobs in M. malaindosinensis; (3) male right P5 Exp-2 with a narrow chitinous flange on the inner margin in M. botulifer versus the more elevated flange

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in *M. malaindosinensis*; (4) right side of female genital double-somite with an obviously botuliform out-growth (cylindrical form with rounded end or sausage-shaped) in M. botulifer versus a small, conical out-growth with a slightly dilated proximal part and gradually tapering to the tip in *M. malaindosinensis*. Thus, the valid status of *M. malaindosinensis* is confirmed. In Thailand, *M. malaindosinensis* is a common species occurring in lakes, permanent ponds, swamps, reservoirs, rivers, and temporary ponds and has been found throughout the country except in the west of Thailand. This species has been reported in Singapore [55] and Cambodia [46]. Recently, *M. malaindosinensis* has been found in two shallow meso-eutrophic and hypereutrophic lakes in Malaysia [26].

Mongolodiaptomus mekongensis Sanoamuang and Watiroyram, 2018 (Figure 4C) was discovered in freshwater ecosystems in the floodplain of the lower Mekong River Basin [20]. It is an uncommon taxon in permanent ponds and swamps but is common in temporary habitats such as rice fields, roadside canals, and temporary ponds in the Ubon Ratchathani Province of northeastern Thailand. This species has so far been recorded in Cambodia, Laos, and Vietnam [20].

Mongolodiaptomus pectinidactylus (Shen and Tai, 1964) (Figure 4D) was originally described as *Allodiaptomus pectinidactylus* from a fish pond on Hainan Island, China [43]. This species was reported for the first time in Thailand. It is a rare taxon and has been found in lakes and temporary ponds in the northeast of Thailand. This species is also found in Vietnam [32] and southern China [38].

Mongolodiaptomus rarus (Ranga Reddy, Sanoamuang and Dumont, 1998) was originally described as *Allodiaptomus rarus* [7]. It is an uncommon species and has been reported only from temporary water habitats in the northeast of Thailand.

Mongolodiaptomus uenoi (Kikuchi, 1936) (Figure 7D) was originally described as Diaptomus uenoi from Taiwan [57] and redescribed by Ranga Reddy et al. (2000) based on specimens from Thailand [8]. It is a fairly common taxon occurring in canals, swamps, reservoirs, rivers, roadside canals, and temporary ponds in the northeast of Thailand. This species has also been reported in Indonesia [8], Vietnam [32], and southern China [38].

Mongolodiaptomus sp. is an extremely rare, undescribed diaptomid found in the northeast of Thailand. It is morphologically similar to *M. mekongensis*. A detailed description of this species will be published separately.

3.3.7. Genus Neodiaptomus Kiefer, 1932

Neodiaptomus laii Kiefer, 1974 was described based on specimens from Malaysia [58]. It is an uncommon species and has been found in canals, ponds, swamps, and temporary ponds in the northeast, east, and south of Thailand. This species is also found in Singapore [28] and Laos [47]. The two following diagnostic criteria of the genus Neodiaptomus are lacking: (1) the principal lateral spine is inserted generally at the middle of the outer margin of the male right P5 Exp-2 and (2) the right caudal ramus with a tooth-like chitinous structure at the inner ventro-distal corner; thus, it is more appropriate to transfer N. laii to the genus Heliodiaptomus.

Neodiaptomus meggitti Kiefer, 1932 was first described in Rangoon, Myanmar [59]. It was redescribed based on specimens from the South Andaman Islands, India, by Ranga Reddy (2000) [60]. *N. meggitti* is an extremely rare species. It was recorded for the first time in Thailand, occurring in a permanent pond in Chiang Rai Province, northern Thailand. It is also found in Malaysia [55].

Neodiaptomus schmackeri (Poppe and Richard, 1892) (Figure 8C) was originally described as Diaptomus schmackeri [61]. Among the 14 reported species of the genus Neodiaptomus [62], N. schmackeri is the most widely distributed species, being reported from southern China, the Russian Far East, Nepal, India, Bangladesh, Sri Lanka, Korea, Japan, Taiwan, the Philippines, Malaysia, Singapore [1,63] and Vietnam [32]. Recently, Alfonso et al. (2014) [64] have reported this species in eight lakes in Albania (Europe) for the first time. Since 2003, this species has most likely been introduced to Kazakhstan's Shardara Reservoir (Central Asia) with imported fish [65]. It is a fairly common species, occurring

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in canals, swamps, rice fields, roadside canals, and temporary ponds in the north, central and west of Thailand.

Neodiaptomus siamensis Proogkiat and Sanoamuang, 2008 was described from specimens recorded in Thailand [18]. It is an extremely rare species and has been found only in three temporary pools in Kamphaeng Phet and Phitsanulok Provinces (these provinces are sometimes designed in the northern region) in the central region of Thailand. This species has not been found in other countries.

Neodiaptomus songkhramensis Sanoamuang and Athibai, 2002 was discovered in several temporary water habitats in the vicinity of the Song Khram River, a tributary of the Mekong River [15]. It is an uncommon species, occurring in rice fields, roadside canals, and temporary ponds in northeastern Thailand. This species has not been reported in other countries.

Neodiaptomus yangtsekiangensis Mashiko, 1951 was described from samples recorded from the Yangtze River, central China [48]. It was redescribed based on specimens from Thailand by Ranga Reddy et al. (1998) [7]. N. yangtsekiangensis is a common species occurring in every type of habitat (except in rice fields) in the northeast, east, and south of Thailand. This species has been reported in southern China [38], Laos, Cambodia [46], and Vietnam [32].

3.3.8. Genus Phyllodiaptomus Kiefer, 1936

The genus *Phyllodiaptomus* Kiefer, 1936 is among the most common freshwater diaptomid copepods in Southeast Asia [9]. Members of this genus are grouped into two subgenera, based on the distinctive structures of the male left P5 Exp-2. The subgenus *Phyllodiaptomus* (*Ctenodiaptomus*) (Dumont, Ranga Reddy and Sanoamuang, 1996) [5] has a serrated hyaline fan on the inner margin of the left P5 Exp-2, while in Phyllodiaptomus (*Phyllodiaptomus*) (Dumont, Ranga Reddy and Sanoamuang, 1996), the corresponding structure bears a field of spinules.

Subgenus Phyllodiaptomus (Ctenodiaptomus)

Dumont, Ranga Reddy, and Sanoamuang, 1996

Phyllodiaptomus (Ctenodiaptomus) praedictus Dumont and Ranga Reddy, 1994 (Figure 2A) was described based on specimens from Thailand [4]. It is a common species inhabiting every type of freshwater habitat throughout Thailand, except in the south. This species has also been recorded in Laos and Cambodia [46]. Another closely related subspecies, Phyllodiaptomus (Ctenodiaptomus) praedictus sulawesensis Alekseev and Vaillant, 2013, has been reported in Lake Tondano, North Sulawesi, Indonesia [31].

Phyllodiaptomus (Ctenodiaptomus) surinensis Sanoamuang and Yindee, 2001 was discovered in two irrigation canals in Surin Province, northeastern Thailand [14]. It is an extremely rare species and has never been found again. This species appears to be an endemic species of Thailand.

Subgenus Phyllodiaptomus (Phyllodiaptomus)

Dumont, Ranga Reddy and Sanoamuang, 1996

Phyllodiaptomus (*Phyllodiaptomus*) *christineae* Dumont, Ranga Reddy, and Sanoamuang, 1996 (Figure 2B) was described based on specimens from Thailand [5]. It is a common species and has been recorded in canals, lakes, permanent ponds, swamps, reservoirs, rivers, and temporary ponds in the north, northeast, central, east, and west of Thailand. This species has not yet been found in the south. This species has also been reported in Laos [46].

Phyllodiaptomus (Phyllodiaptomus) roietensis Sanoamuang and Watiroyram, 2020 (Figure 2D) was described based on specimens from Thailand and Cambodia [21]. It is a rare species, inhabiting rice fields, roadside canals, and temporary ponds only in the northeast of Thailand.

Phyllodiaptomus (Phyllodiaptomus) thailandicus Sanoamuang and Teeramaethee, 2006 (Figure 2C) was described based on specimens from Thailand [17]. It is a rare species oc-

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curring in permanent and temporary ponds in the northeast and the south of Thailand. This species appears to be an endemic species of Thailand.

Phyllodiaptomus (*Phyllodiaptomus*) sp. is a rare, undescribed diaptomid in the northeast of Thailand. It is similar to *P.* (*P.*) *christineae*. A description of this species will be published in a separate article.

3.3.9. Genus Tropodiaptomus Kiefer, 1932

Tropodiaptomus hebereri (Kiefer, 1930) (Figure 6A) was originally named as *Diaptomus hebereri* [66]. It is an extremely rare taxon that occurs in canals in the north of Thailand. This species has been found in Malaysia [67], Singapore [3], India [68], Indonesia [31], and China [38].

Tropodiaptomus lanaonus Kiefer, 1982 was described from Lake Lanao, Mindanao Island, Philippines [69]. It was recorded as an endemic diaptomid of the Philippines by Lopez et al. (2017) [30]. *T. lanaonus* is a rare species and has been reported from lakes in the northeast and central regions of Thailand.

Tropodiaptomus megahyaline Saetang, Sanoamuang, and Maiphae, 2020 is a newly described species from Thailand [22]. It is a rare species and has been reported from rice fields and permanent ponds in the northeast of Thailand. This species was recorded as *Tropodiaptomus* sp. in Lake Bueng Khong Long in Bueng Kan Province, northeastern Thailand by Teeramaethee (2006) [70].

Tropodiaptomus oryzanus Kiefer, 1937 (Figure 6B,C) was described based on samples from rice fields in Taiwan [71]. It is an uncommon species and has been found in lakes and temporary habitats such as rice fields, roadside canals, and temporary ponds in the northeast of Thailand. This species is also found in Vietnam [32], China, Korea, and Japan [38].

Tropodiaptomus ruttneri (Brehm, 1923) (Figure 6D) was originally named Diaptomus ruttneri, based on specimens from Yunnan Province, China. It is an uncommon species and has been reported from rice fields and temporary ponds in the north and northeast of Thailand. This species is also known from Malaysia [67], Japan, and Taiwan [3].

Tropodiaptomus vicinus (Kiefer, 1930) (Figure 6E) was originally described as Diaptomus vicinus based on specimens from Indonesia [72]. It is a common species and has been found in irrigation canals, lakes, permanent ponds, swamps, and rivers in the north, northeast, central, west, and south of Thailand. This species has been found in the Philippines [3], Malaysia [67], Cambodia [46], Indonesia [31], India [68] and Vietnam [32].

Tropodiaptomus sp. is an extremely rare, undescribed diaptomid collected from a temporary pond in the north of Thailand. Morphologically, it is similar to *T. ruttneri*. A description of this species will be published separately.

3.3.10. Genus Vietodiaptomus Dang, 1977

The genus *Vietodiaptomus* was created based on specimens from Vietnam, with *Vietodiaptomus hatinhensis* Dang, 1977 as the type species [73]. According to Walter and Boxshall (2021), the other two members of this genus are *Vietodiaptomus blachei* (Brehm, 1951) and *Vietodiaptomus tridentatus* Dang and Ho, 1985 [62]. Since the description of this genus was published in the Vietnamese language, a redescription using English is required.

Vietodiaptomus blachei (Brehm, 1951) (Figure 8A) was originally described as Eodiaptomus blachei based on specimens from Cambodia [23]. It is a common species occurring in canals, lakes, permanent ponds, swamps, reservoirs, rice fields, roadside canals, and temporary ponds, and has been recorded in the north, northeast, central, west, and south of Thailand. This species has not yet been found in the eastern region. This species has been reported from Indonesia [3], Laos [47], Malaysia [67], and Singapore [28].

Subfamily Paradiaptominae Kiefer, 1932

Genus Paradiaptomus Sars, 1895

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Paradiaptomus greeni (Gurney, 1906) (Figure 5C,D) was originally described as Diaptomus greeni based on samples from Sri Lanka (Ceylon) [74]. It is also found in South Africa [75], Tunisia [76], India [77], and China [38]. It is an extremely rare species and has been found so far only in a temporary pond in Khon Kaen Province, northeastern Thailand. This is the first record of a representative of the Paradiaptominae in Southeast Asia.

4. Discussion and Conclusions

The species diversity of freshwater diaptomid copepods (42 species) in Thailand is higher than that reported from the other Southeast Asian countries—8 from the Philippines [30], 12 from Malaysia and Singapore [25], 17 from Indonesia [31], 19 from Laos [24], 24 from Cambodia [46], and 29 from Vietnam [32]. The comparison with other Asian countries revealed that the diaptomid diversity of Thailand is higher than Kazakhstan (26 species) [65] but comparable to that of India (about 50 species) [77] and China (56 species) [38], although the country areas of India and China are larger than Thailand by 6.4 and 18.7 times, respectively. Thus, Thailand is one of the countries with the most diversified diaptomid fauna in the world, and it is a biodiversity hotspot for diaptomid copepods in Southeast Asia.

The new record for Thailand (*Paradiaptomus greeni*) predominantly occurs in Africa but is also known in other Asian countries, including Sri Lanka, India [75], and the Nanning Province of southern China [38]. It is noted that we did not find two species—*Tropodiaptomus doriai* and *Sinodiaptomus chaffanjoni*—in our extensive collection. Both species were previously recorded in Thailand by Daday (1906) [34] and Boonsom (1984) [35], respectively.

Thailand has a greater record of co-occurrence (up to seven species) than India's Northern Western Ghats (up to four species) [77]. The high degree of diaptomid species co-occurrence in Thailand is remarkable, as it is uncommon to find more than one calanoid species in a temperate lake [78]. The difference in diversity might also be partly a result of artefacts due to more intensive surveying and a good basis in systematics and taxonomy in Thailand within the region.

The species richness of diaptomid copepods (35 species) in the northeast, which is higher than in the other regions of Thailand (8–17 species), can be explained by the fact that it covers about one-third of the country and contains many temporary water bodies in the floodplains of major rivers, and the majority of the samples (about 60%) were collected from this region.

In conclusion, a total of 4962 samples were analyzed from 2150 diverse freshwater habitats across Thailand, and 42 species belonging to 11 genera in 2 subfamilies of Diaptomidae were identified. The current number of species listed is the highest among those reported in other Southeast Asian countries, ranging from 8 to 29. Mongolodiaptomus is the most diverse genus with 10 species, followed by Tropodiaptomus with 7, and Neodiaptomus and *Phyllodiaptomus* with 6. In total, 17 species (40.5% of the species recorded) have been described originally from Thailand since 1994. Eight taxa (Arctodiaptomus sp., Mongolodiaptomus pectinidactylus, Neodiaptomus meggitti, Tropodiaptomus hebereri, T. lanaonus, T. oryzanus, T. ruttneri, and Paradiaptomus greeni) are recorded for the first time in Thailand. This is the first record of a species (P. greeni) in the subfamily Paradiaptominae in Southeast Asia as well. The relative occurrences of the species recorded are categorized into five groups: 12 common, 5 fairly common, 9 uncommon, 7 rare, and 9 extremely rare species. The most frequently encountered species in the sampled localities, which are widely distributed throughout the six regions of Thailand, were Mongolodiaptomus botulifer, Phyllodiaptomus praedictus, M. calcarus, M. dumonti, M. malaindosinensis, Vietodiaptomus blachei, P. christineae, Eodiaptomus sanoamuangae, Neodiaptomus yangtsekiangensis, E. draconisignivomi, Tropodiaptomus vicinus, and Heliodiaptomus elegans. The species richness of the diaptomids ranged from 1 to 7 species per locality at the same sampling dates. The coexistence of 4–7 diaptomid species has been observed in northeastern Thailand, particularly in small-sized

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temporary-water habitats. The high degree of diaptomid species co-occurrence in Thailand is remarkable, as it is uncommon to find more than one calanoid species in a temperate lake. Eight species appear to occur only in temporary waters. The northeast is the most diverse region, with 35 recorded species. Twelve species appear to be endemic to Thailand, and eight are endemic to the lower Mekong River Basin countries (Thailand, Cambodia, Laos, and Vietnam). This study demonstrated that species di-versity is high in temporary water habitats in the floodplains of major rivers, and Thailand is a biodiversity hotspot for diaptomid copepods in Southeast Asia. In addition, the taxonomic status of *Mongolodiaptomus malaindosinensis* has been confirmed.

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