RAFFLES BULLETIN OF ZOOLOGY **62**: 339–351
Date of publication: 30 May 2014
http://zoobank.org/urn:lsid:zoobank.org:pub:D576585B-1DCD-40A8-831F-1408698EA7D9

Brooding behaviour of the centipede *Otostigmus spinosus* Porat, 1876 (Chilopoda: Scolopendromorpha: Scolopendridae) and its morphological variability in Thailand

Warut Siriwut[1, 2], Gregory D Edgecombe[3], Chirasak Sutcharit[2] & Somsak Panha[2*]

Abstract. Maternal care is shared by three of the five living orders of centipedes and is generally thought to have a single evolutionary origin in this group. Literature on brooding behaviour in the order Scolopendromorpha is scattered, with observations available for six genera. Brooding in the diverse genus *Otostigmus* Porat, 1876, with ca 120 species mostly distributed in the tropics, has been documented in only two species from Brazil. Six broods of *O. spinosus* representing different embryonic and adolescent (post-embryonic) stages are documented from southern Thailand. Size of the brood is similar to other species of *Otostigmus*, and this species exhibits filial cannibalism also documented in the Neotropical *O. scabricauda*. *Otostigmus spinosus* is redescribed with emphasis on a large sample of Thai material and is reported from Laos for the first time. Sexual dimorphism is apparently exhibited by a distal projection on tarsus 1 of legs 20 and 21 in males. Considerable variability in taxonomic characters within and between populations renders a consistent distinction from *O. punctiventer* (Tömösváry, 1885) less clear-cut than previously suspected.

Key words. Maternal care, Scolopendromorpha, Otostigminae, Thailand

INTRODUCTION

Parental investment appears both in invertebrates and vertebrates. In terrestrial arthropods, this behaviour is classified into three forms: female uni-parental (maternal) care, male uni-parental (paternal) care, and bi-parental care. There are many reports of terrestrial arthropod groups exhibiting these behavioural characteristics, among them arachnids, insects, millipedes, and centipedes (Zeh & Smith, 1985). Centipedes are a terrestrial arthropod group that plays an important role in ecosystems as top consumers in the trophic level of soil macroinvertebrates. In the case of extant orders, parental care behaviour and brooding are limited to three orders: Craterostigmomorpha, Scolopendromorpha, and Geophilomorpha (Bonato & Minelli, 2002; Edgecombe & Giribet, 2007), and this behaviour has led to heightened interest in these animals. In the order Scolopendromorpha, brooding and maternal care have been reported in six genera; *Scolopendra* Linnaeus, 1758, *Cryptops* Leach, 1815, *Cormocephalus* Newport, 1844, *Scolopocryptops* Newport, 1844, *Rhysida* Wood, 1862, and *Otostigmus* Porat, 1876 (Lewis, 1981; Bonato & Minelli, 2002; Chao, 2008; Mitić et al., 2012). The scolopendrid genus *Otostigmus*, the subject of the present study, is widely distributed in tropical areas. It is a diverse group, with approximately 120 described species in three subgenera (Minelli et al., 2006 and onwards). Most of them live in leaf litter, coastal forest, and rotting wood; occasionally, however, they are also found in human habitations.

Presently, there are very few reports about development and brooding behaviour of *Otostigmus*, only two species having been studied, both in the New World/African tropical subgenus *O.* (*Parotostigmus*): *O.* (*P.*) *tibialis* Brölemann, 1902 and *O.* (*P.*) *scabricauda* (Humbert & Saussure, 1870), both from Brazil. Bücherl (1971) provided succinct accounts of maternal care in these species. The mother constructs a brood chamber to lay eggs in a dark, protected area. The cluster of eggs consists of 15–30 individuals, of yellowish colour, and 1–2 mm in diameter. During brooding, the mother remains coiled around the hatchlings until the young leave. Machado (2000) gave a more detailed account of brooding by *O. scabricauda* based on a sample of three egg clusters and six first instar hatchling clusters.

In this paper, we present observations on maternal care behaviour and the brooding period in natural habitats for *Otostigmus* in Thailand. The documented species is *Otostigmus spinosus*, originally described from Java and until now known from eastern India, Burma, Vietnam, Peninsular Malaysia, Singapore, and Indonesia (Sumatra and Krakatau as well as Java) (Schileyko, 2007; Lewis, 2010). It is reported here for the first time from Thailand and Laos. The aims of this study are to describe maternal care during

[1]Biological Sciences Program, Faculty of Science, Chulalongkorn University, Phayathai Road, Bangkok 10330, Thailand

[2]Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand; Email: somsak.pan@chula.ac.th (*corresponding author)

[3]Department of Earth Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

the brooding period and to provide comparative data for some external morphological characters between hatchlings and their mothers to clarify changes in taxonomic characters during post-embryonic development. Also, the distribution and description of Thai *O. spinosus* are given based on the range of variation in traditionally employed taxonomic characters for *Otostigmus*. Variability in these characters creates problems for taxonomists to identify the limits of species within this species-rich genus. Some taxonomic characters may be affected by such factors as geographic and individual variation, regeneration, and changes through growth (Lewis, 1978).

MATERIAL AND METHODS

Specimen collection. Centipedes were collected and observed in natural habitats throughout Thailand during 2012–2013. In the field, hand sorting was used to collect and characteristics of the animals' habitats were recorded. GPS coordinates for each locality are provided. Collected specimens were fixed in 95% ethanol and are housed in the Chulalongkorn University Museum of Zoology, Bangkok (prefix CUMZ).

Behavioural study. Behaviour was recorded and photographed only in natural habitats. Behavioural postures were recorded during the first 15 minutes after discovering animals in a brood chamber. Video recording was performed by using DSLR and pro-compact digital cameras (Nikon D700 and Canon G12). After observation, most of the brooding centipedes were collected and preserved in 95% ethanol. Descriptions of parental care are given. A brooding behaviour scheme of *O. spinosus* was made by integrating data from our observations and comparing with previous behavioural literature on Scolopendridae.

Systematics and comparative morphological studies. Taxonomic study has been conducted with reference to standard monographs (Attems, 1930a) and the most recent revisions (Lewis, 2010). Nomenclature for taxonomic characters is based on standard terminology for centipede external morphology by Bonato et al. (2010). Specimens from Thailand were compared with specimens deposited in the Natural History Museum, London, and also compared with holotype descriptions in recent revisions of *Otostigmus* species. Drawings were made to depict variability in taxonomic characters of all atypical specimens. For comparative study, traditional taxonomic characters of this species have been recognised and compared between the mother and hatchlings. Developmental stages of hatchlings have been recorded and identified by using previous literature on post-embryonic development of Scolopendridae. Variable characteristics have been recorded and photographed by using the Cell'D© program connected with an Olympus stereomicroscope.

RESULTS

Description of broods and maternal care behaviour. The patterns of development of scolopendrids have been described using different schemes. Drawing upon *Scolopendra cingulata* and *S. dalmatica*, Heymons (1901) recognised a first embryonic stadium, a foetus or intermediate stadium, and an adolescent stadium, based on observations on moulting. Subsequently, Lawrence (1947) divided the phase of maternal care in *Cormocephalus multispinus* into two parts that consist of six stages, these comprising three embryonic stages and three adolescent stages based on morphological characteristics (summarised by Lewis, 1981). The same six stages were described for *Cormocephalus anceps* by Brunhuber (1970).

Six broods of *O. spinosus* were found in this survey (Fig. 2A–F). Dates of collection are as follow: brood A (9 October 2012); brood B (10 October 2012); broods C–F (9 August 2013). Their habitats are diverse, including under broken roof tiles near a residential resort (brood A), under a clump of moss (brood B), and under coconut shells on the soil surface near human habitats (broods C–F). All collecting localities are located in the southern part of Thailand which had very high humidity and storms on some occasions. The distribution and schematic of brooding behaviour of *O. spinosus* in Thailand are given in Figs. 1 and 4, respectively.

Brood A (Fig. 2B): After clearing the surface of the brood chamber, we found hatchlings, with morphology corresponding to the second adolescent stage sensu Lawrence (1947) (see Table 1 for morphological comparison of the mother and adolescents). The mother (body length 26 mm) was coiled around a brood of 19 hatchlings. When disturbed she moved to find a new place to hide in an adjacent area, leaving the hatchlings two or three times. The mother subsequently returned and carried the hatchling cluster to the new place using her forcipules (Fig. 3D) and anterior

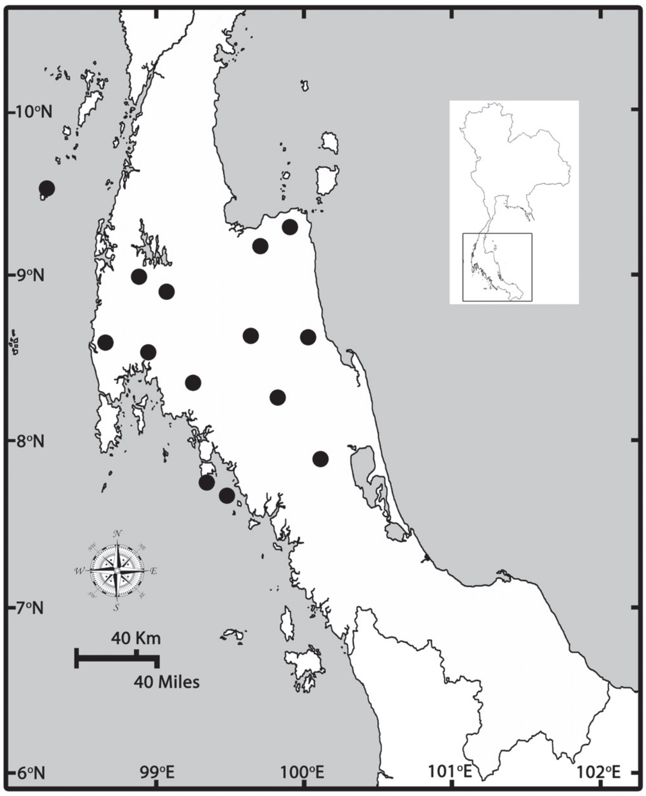

Fig. 1. Distribution of *Otostigmus spinosus* Porat, 1876 in southern Thailand.

Table 1. Comparison of traditional taxonomic characters between adult female and 2nd adolescent stadium *O. spinosus* (samples from Brood A). * refers to character in damaged condition, ? refers to unclear character

Taxonomic Characters	**Specimens**				
	Mother	**Hatchling 1**	**Hatchling 2**	**Hatchling 3**	**Hatchling 4**
No. of antennal articles	23/21	18/19	19/17	18/18	15*/18
No. of glabrous articles	2.5/2.3	2/2	2/2	2/2	2.5/2.5
No. of forcipular teeth	4+4	4+4	4+4	4+4	4+4
Paramedian suture complete from tergite No.	5	6	6	6	4
Margination starting from tergite No.	11	11	11	11	11
Sternal paramedian sutures	Incomplete	?	?	?	?
Number of apical spines on coxopleuron	2	1	1	1	2
Number of lateral spines on coxopleuron	2	2	1	1	1
Number of dorsal spine on coxopleuron	1	1	?	?	?
Length of coxopleural process	Moderate length VL-5	Moderate length V-4	Moderate length VL-4	Moderate length VL-4	Moderate length VL-
Prefemoral spine formula of ultimate leg	VL-4 VM-3 DM-2	V-2 VM-2 DM-2	V-3 VM-3 DM-2	V-3 VM-3 DM-2	V-3 VM-3 DM-2
No. of corner spines on prefemoral process of ultimate legs	2+2	1+1	1+1	1+1	1+1
Legs No. with 2 tarsal spurs	1–3	1–4	1–3	1–4	1–4
Legs No. with tibial spur	1	?	?	?	?
Leg 20 with prefemoral process	1+1	1+?	absent	1+1	1+1

legs to hold part of the hatchling cluster under her head and the ventral side of her body (Fig. 3E). All individuals were collected but the cluster of hatchlings had already dispersed and some had disappeared, with only six hatchlings and the mother surviving. The disappearance of hatchlings suggests filial cannibalism, as has been directly observed in brood F (see below).

Brood B (Fig. 2A): The hatchlings in this brood were at the third embryonic stadium (sensu Lawrence, 1947), covered by egg shell (see brood E for description). There were 27 hatchlings in the brood chamber with their mother (Fig. 2A). The mother exhibited body posture as an S-shape over the upper part of the hatchling cluster (Fig. 3C). She occasionally exhibited falcate coiling (Fig. 3B) or simple loop coiling (Fig. 3A) around the hatchlings, and adjusted their position on her ventral surface using the forcipules. After observation, five hatchlings were collected, the remainder being returned to the brood chamber.

Brood C (Fig. 2C): This brood consisted of 19 cleavage stage eggs. All of them were coated with thin, sticky mucous that combined all together as a massive cluster. The mother (body length 32 mm) nestled her eggs and carried the egg cluster under her body using locomotory legs. The mother's posture switched between a simple loop and an S-shape.

Brood D (Fig. 2D): The hatchlings were at the first adolescent stage. They are white in colour, and the antennae have scattered, short setae. Coxosternal teeth, paramedian sutures on the tergites and sternites, spurs on the locomotory legs and ultimate legs, and the coxopleural process spines are undeveloped. The posture of the mother (body length 33 mm) was a simple loop for the first five minutes after exposure of the nest; subsequently, S-shape posture and falcate coiling were exhibited. Subsequently, the mother moved to find a new location. The cluster of hatchlings (20 individuals) was moved to the ventral posterior part of her body. Locomotory and ultimate legs were used to reposition and protect the hatchling cluster during the search for a new nest position.

Brood E (Fig. 2E): This brood contained 21 hatchlings at the third embryonic stage, as was brood B. The number of antennal articles is consistently 17, the tergites and sternites are fully segmented but weakly sclerotised and colourless, the ocelli are distinct but unpigmented and the legs are articulated but lack pretarsal claws. The mother (body length 36 mm) surrounded the hatchling cluster in an S-shape posture. Most of the hatchlings were covered by the ventral side of the mother's body but two of them had been separated from the brood.

Brood F (Fig. 2F): The mother (body length 35 mm) exhibited S-shape posture, partially covering the eggs. The eggs were at the first embryonic stage (sensu Lawrence, 1947), 16 eggs being present. The eggs lay on the soil surface for a while and afterwards the mother used the forcipules to collect them under her body and coil round them. The mother displayed filial cannibalism, eating some embryos after recollecting the cluster (Fig. 3F).

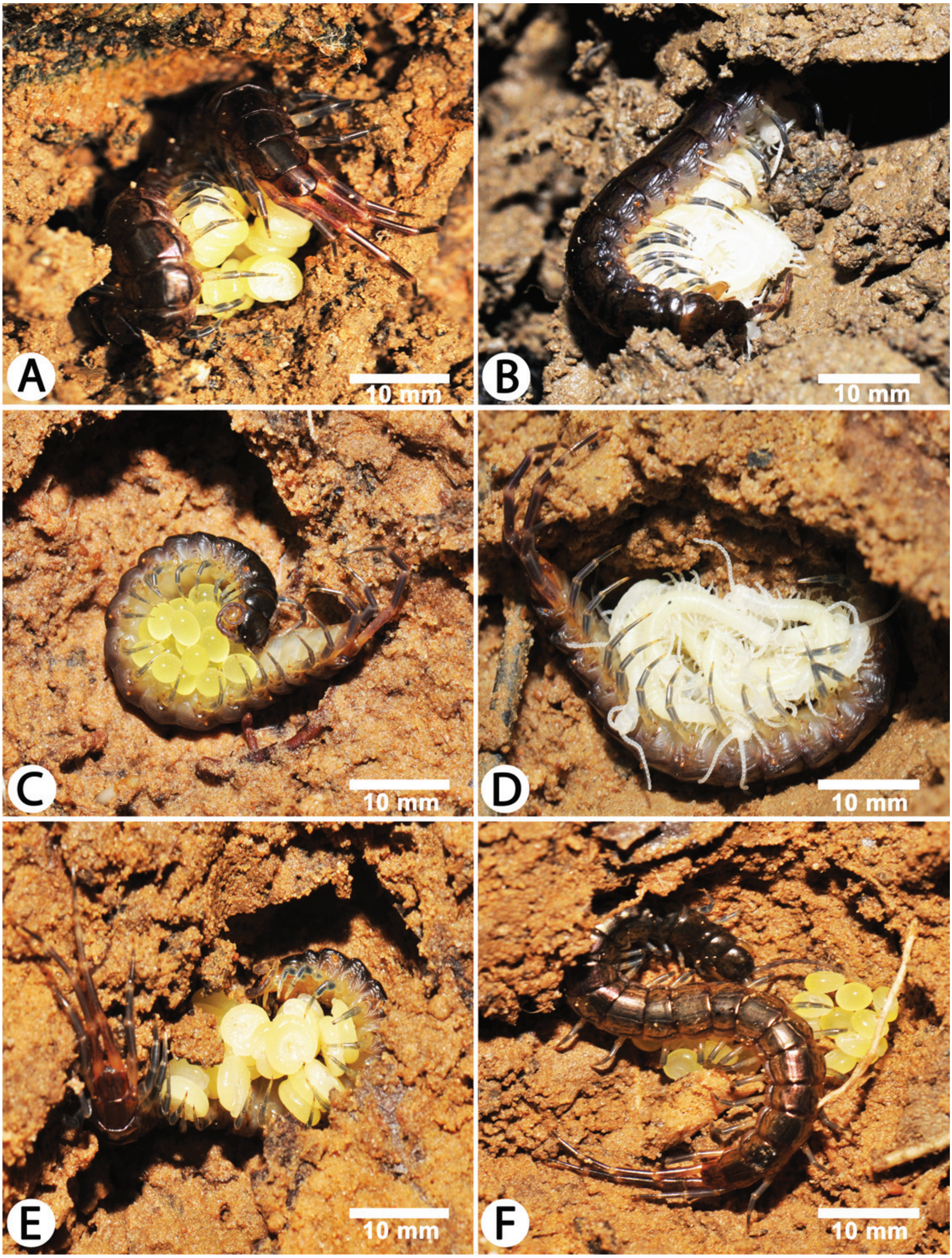

Fig. 2. Six broods of *Otostigmus spinosus*: A, Brood sample from local resort near Khao Sok National Park, Surat Thani province; B, Brood sample from Wat Tham Wararam, Surat Thani province; C–F, Brood samples from Wat Tham Phung Chang, Phang-nga province.

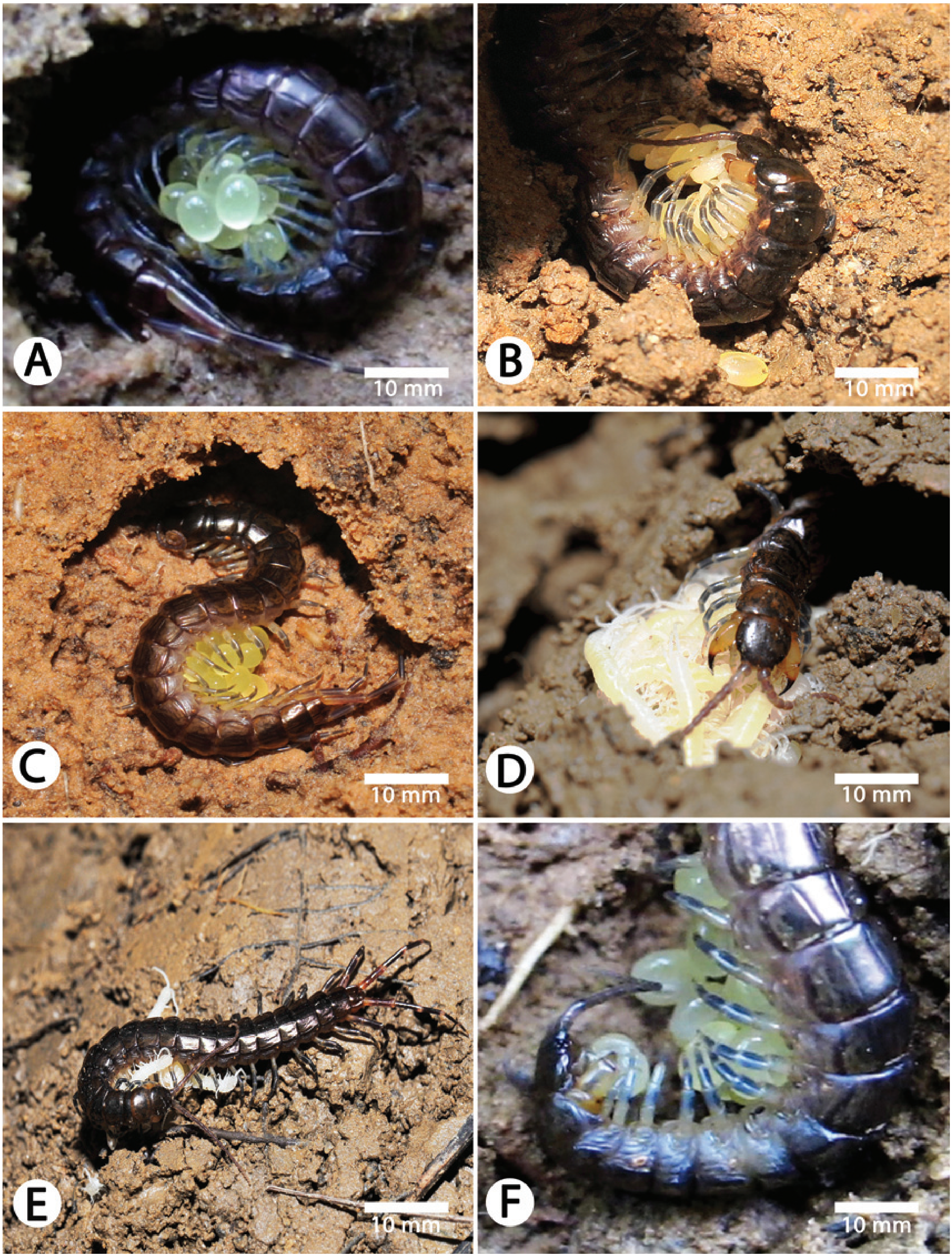

Fig. 3. Brooding behaviour of *Otostigmus spinosus*. A–C, Orientation of mother with cluster of hatchlings; A, Simple loop; B, Falcate coiling; C, S-shape posture; D, Forcipules being used by mother to catch 2nd adolescent stage hatchlings; E, Mother moving and carrying cluster of 2nd adolescent stage hatchlings under her body; F, Mother exhibiting filial cannibalism of 1st embryonic stage.

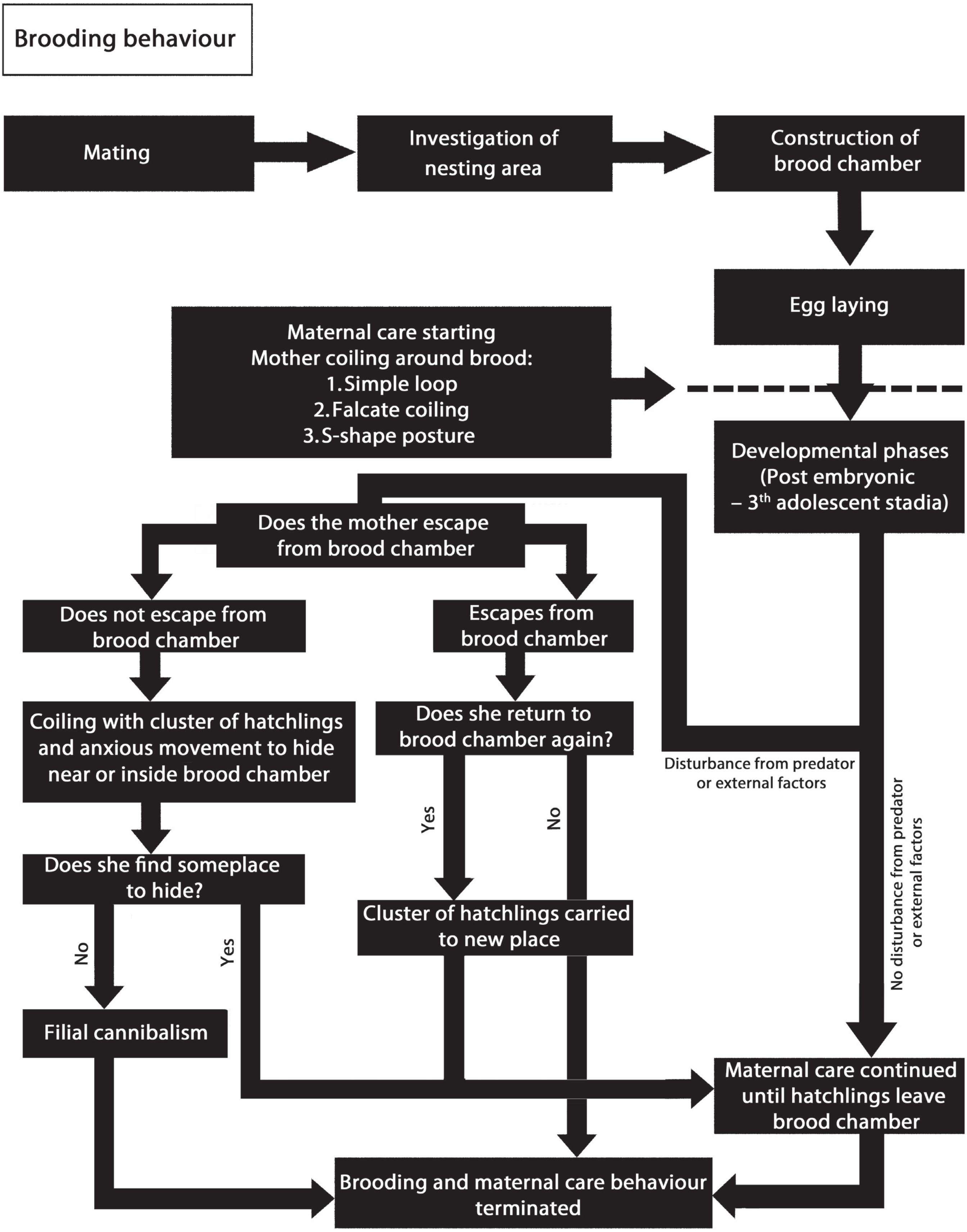

Fig. 4. Schematic of brooding behaviour of *Otostigmus spinosus*.

TAXONOMY

Family Scolopendridae Leach, 1814

Subfamily Otostigminae Kraepelin, 1903

Genus *Otostigmus* Porat, 1876

Type species. *Otostigmus carinatus* Porat, 1876; by subsequent designation of Pocock (1891a).

Otostigmus spinosus Porat, 1876
(Figs. 5, 6)

Otostigmus spinosus Porat, 1876: 22
Branchiotrema nitidulum Tömösváry, 1885: 26, table 3, figs. 19, 20
Otostigmus spinosum: Haase, 1887: 71, Taf. 4, fig. 70a–d
Otostigmus spinosum ab. *hirtipes* Haase, 1887: 71, Taf. 4, fig. 71a–c
Otostigma spinosum: Pocock, 1891b: 414; Pocock, 1894: 312
Otostigmus spinosus: Kraepelin, 1903: 116, fig. 53; Kraepelin, 1904: 247; Attems, 1930a: 152, fig. 182; Attems, 1930b: 118; Verhoeff, 1937: 212; Chamberlin, 1939: 3; Chamberlin, 1944: 1; Lewis, 1991: 340, figs. 11–14; Khanna, 1994: 467; Lewis, 2001: 37, figs. 75–78; Khanna, 2001: 206; Schileyko, 2007: 81, fig. 5; Lewis, 2010: 6, figs. 8–13
nec *Otostigmus* (*O.*) *spinosus*: Lewis, 1982: 365, figs. 25–31; Lewis, 1984: 37, fig. 3.15

Type locality. Indonesia: Java.

Distribution. Java, Sumatra, New Guinea, Burma, Laos, Thailand, Vietnam, Malaysia, India?

Material examined. Malaysia: BMNH 1898.9.15.75–76 general collection, 2 of 3 specimens in tube labeled "*Otostigmus* sp." from Penang. **Laos**: CMUZ 00232, one specimen from Ban Kra-Som, Attopue, Laos (15°0'27.2" N 106°51'14.6" E). **Thailand**: CUMZ 00224, one specimen from Wat Tham Wararam, Phanom district, Surat Thani (8°53'2.7" N 98°40'1.4" E). CUMZ 00228, two specimens from Khao Sok, Phanom district, Surat Thani (8°53'37.3" N 98°33'107" E). CUMZ 00225, five specimens from Wat Kerewong, Thap Put district, Phang-nga (8°31'54.8" N 98°34'37.8" E). CUMZ 00226, one specimen from Sairung waterfall, Takua Pa district, Phang-nga (8°44'28.3" N 98°16' 43.1" E). CUMZ 00231, 53 specimens from Surin islands, Phang-nga (9°26'41" N 97°53'30.3" E). CUMZ 00230, one specimen from Sichon district, Nakhon Si Thammarat (9°5'31.4" N 99°54'23.2" E). CUMZ 00229, three specimens from Tham Wang Thong, Khuan Khanun district, Phatthalung (7°40'53.5" N. 100°0'56.6" E.). CUMZ 00223, one specimen from Tham Sumano, Srinagarindha district, Phatthalung (7°35'11.9" N 99° 52'3.2" E), CUMZ 00227, one specimen from Huaito waterfall, Khao Phanom district, Krabi (8°13'35.5" N 98°53'2.5" E).

Diagnosis. 17–22(24) antennal articles, basal 2.3–2.8 articles glabrous dorsally. Forcipular coxosternum with 4–6 main teeth. Forcipular trochanteroprefemoral process with one apical and two inner teeth. Tergite surface smooth, without keels, but with scattered small spines or setae; paramedian sutures starting from TT4–7 and complete margination from TT7–15. Tergite of ultimate leg-bearing segment with or without depression. Sternites with incomplete paramedian sutures occupying 10–30% of anterior part of sternite, posterior part with shallow depression. Posterior margin of sternite of ultimate leg-bearing segment concave, lateral margins converging. Coxopleural process with one to three apical spines, one sub-apical or none, one lateral or none, and one dorsal spine. Ultimate legs long and slender, spine formula on prefemur VL-4 or 5, VM-2–4, M-2–5 and DM-1–4 (including corner spine). Locomotory legs with two accessory spurs; legs 1–3 to 1–5 in equal frequency (rarely 2, 6 or 7) with two tarsal spurs, legs 5–21 (rarely 3, 7 and 8) with one tarsal spur. One tibial spur on legs 1–3 (rarely leg 4). Femoral spur only on leg 1. Dorsal side of leg 20 with one spine at end of prefemur.

Description. Maximum body length approximately 38 mm. Body colour of living animal greenish black except tergite of ultimate leg-bearing segment, which is reddish black. Trochanteroprefemur yellowish white or light brown. Legs light blue or purple except prefemur, which is light yellow. Cephalic plate without sulci or sutures. Preserved specimens dark purple.

Antennae with 17–22 articles (Fig. 5C), 24 articles in one specimen. Basal 2.5–2.8 articles glabrous dorsally (Fig. 6B); atypically 2.3. Basal 2.5–2.8 articles glabrous ventrally (Fig. 6A). Antennae reach segments 4–6 (5 or 6 in large specimens). Forcipular trochanteroprefemoral process bearing one apical and two inner teeth (rarely 3; see Figs. 6D–E). Coxosternal tooth plate wider than long with 4, 5 or 6 main teeth in equal frequency (rarely 3 or 7; see Fig. 6C–F), separated into two groups; inner three or four teeth usually fused and outer 1 or 2 acute (Figs. 5B, 6C, 6F), basal part with one transparent, fine seta on each side, atypically with 1 transparent spine and 2 small spines in a depression (Fig. 6F). One specimen shows an abnormal condition with both tooth plates fused together (Fig. 6D). Coxosternum lacking median suture in some specimens (Fig. 6D), median diastema reaching to base of tooth plate, connecting with basal oblique sutures (Fig. 6C, 6E, 6F). Angle of basal oblique sutures ca 105–110°. Telopodite 2 of second maxilla with one strong transparent spine on each side.

First tergite overlapping cephalic plate, without transverse sulcus (Fig. 5A). Tergites with paramedian sutures complete from TT5 to 6 (rarely TT7); margination typically starting on TT11 to 15 (atypically TT9–10). Tergite surface (Figs. 5D, 6G) with oblique suture anteriorly on TT3 to 5 and with paramedian sulci on TT3 or 4 to 18 (to TT19 to 20 in large specimens). Tergite of ultimate leg-bearing segment (Fig. 6L) usually with median furrow on posterior part (rarely absent). Sternites (Fig. 5E) with short paramedian sutures on anterior part, occupying 10–30% length of sternite. Surface of some sternites with small scattered setae and depressions grouped in triangular arrangement (one atypical specimen with depression continued behind end of paramedian suture), all mostly found on posterior part of sternite (Fig. 6H). Sternite of ultimate leg-bearing segment (Fig. 6K) with sides converging posteriorly, posterior margin concave (one specimen with depression on surface). Oval spiracles present on segments 3, 5, 8, 10, 12, 14, 16, 18 and 20 (Fig. 5F–H).

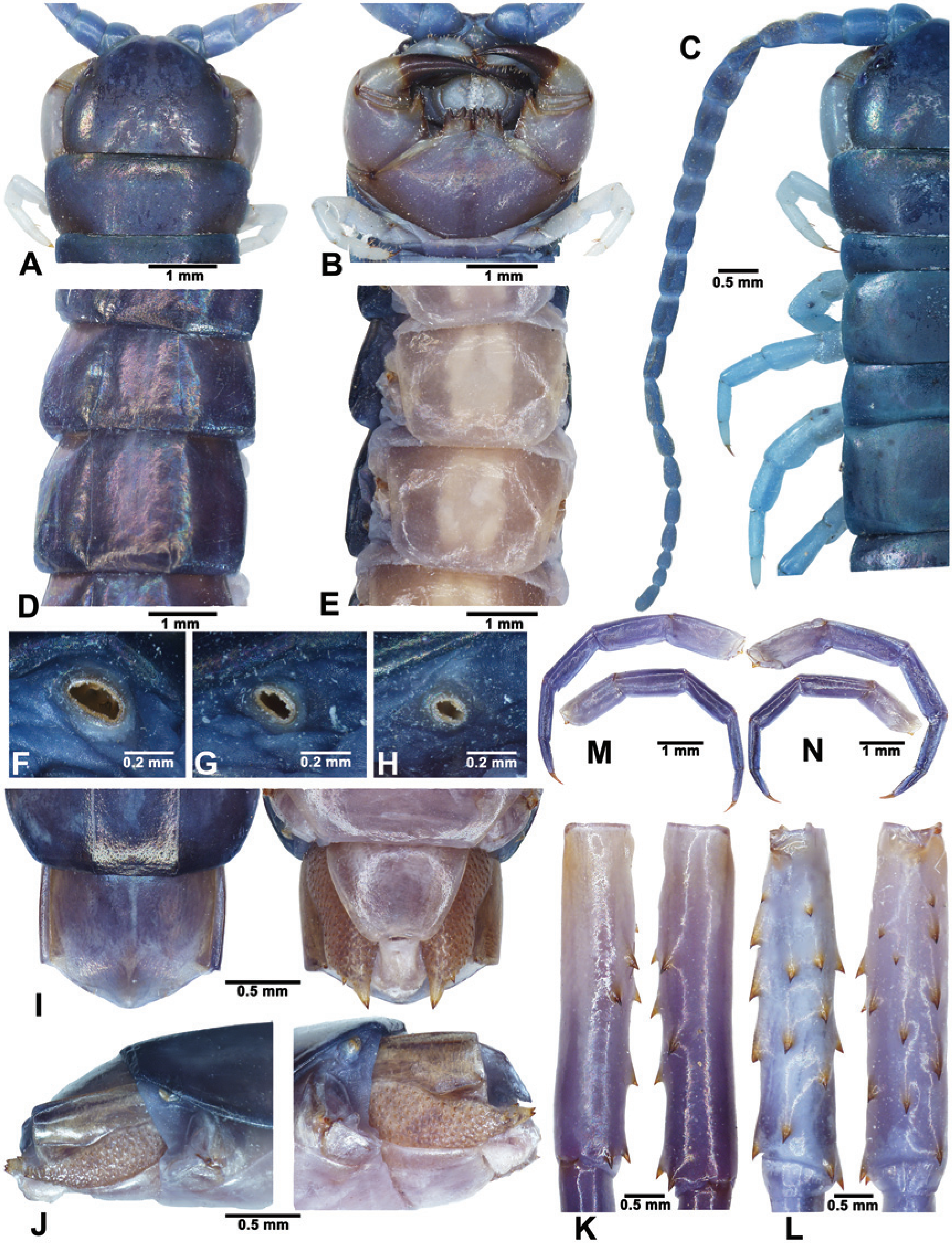

Fig. 5. *Otostigmus spinosus* Porat, 1876. Light photographs of specimens from southern Thailand (Fig. A–E; specimens from Surin Islands, Phang-nga province: CUMZ 00231; Fig. I–N; specimens from Wat Tham Wararam, Surat Thani province: CUMZ 00224). A, Cephalic plate and T1 with first pair of locomotory legs; B, Forcipular segment; C, Antenna with cephalic plate and TT1–5; D, Tergites 9–10; E, Sternites 9–10; F–H. Spiracles on segments 3, 5 and 8, respectively; I, Tergite and sternite of ultimate-leg bearing segment; J, Pore field on left and right coxopleura; K, Dorsal view of ultimate leg prefemur; L, Ventral view of ultimate leg prefemur; M–N, Leg 20 left and right with spine on distal part of prefemora.

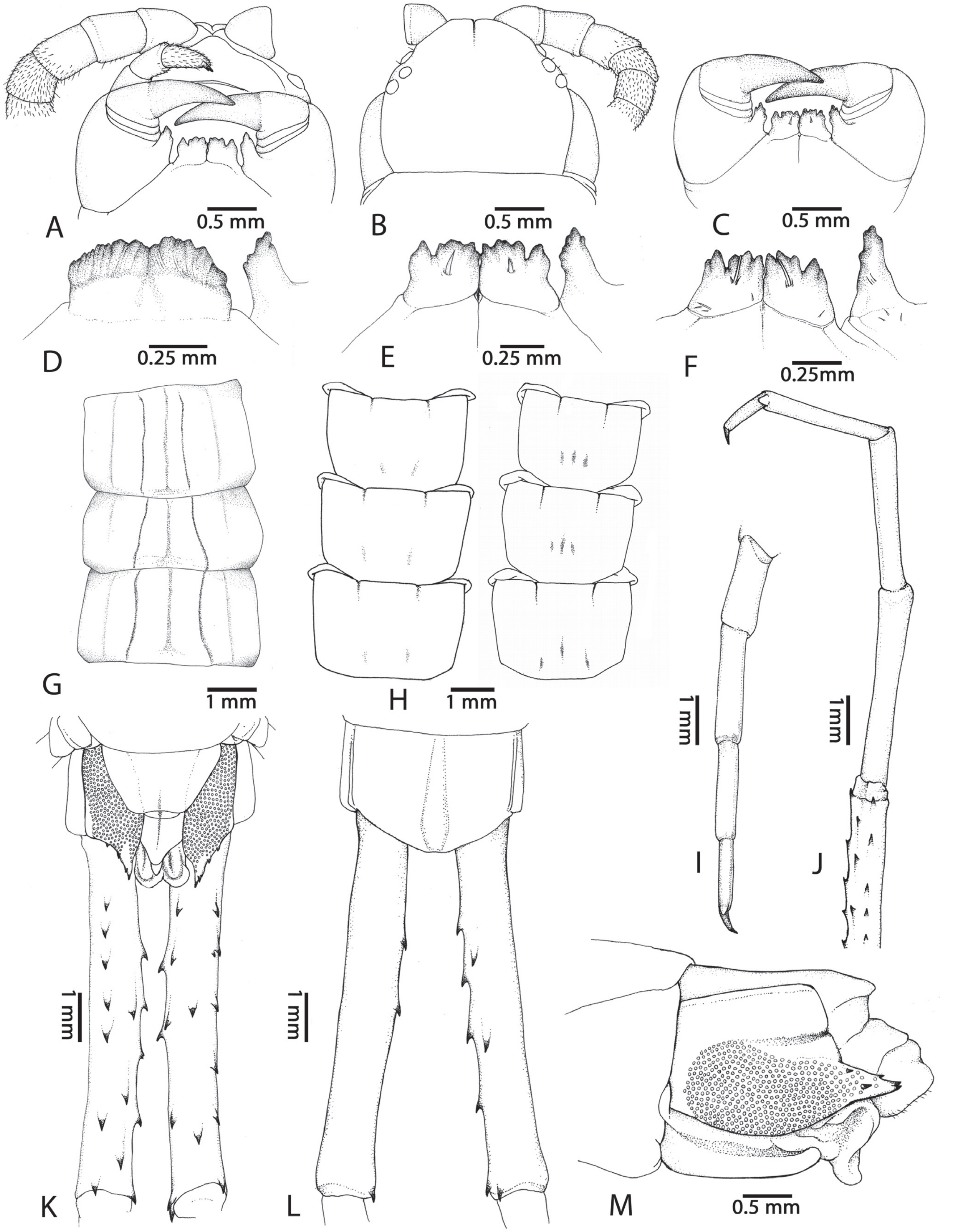

Fig. 6. Variability in taxonomic characters in *Otostigmus spinosus* Porat, 1876 (examination materials: CUMZ 00224, Wat Tham Wararam, Phanom district, Surat Thani; CUMZ 00229, Tham Wang Thong, Phatthalung; CUMZ 00231, Surin Islands, Phang-nga). A, Ventral view of cephalic plate and antenna; B, Dorsal view of cephalic plate and antenna; C, Coxosternite; D–F, Variation in coxosternal teeth; G, Surface of TT5–7; H, Variability of depressions on surface of sternites 5–7; I, Leg 20 with projection on distal end of tarsus 1; J, Leg 21 with projection on tarsus 1; K, Ultimate leg-bearing segment, ventral view, with arrangement of ventral spines on prefemur of ultimate legs; L, Tergite of ultimate leg-bearing segment with arrangement of dorsal and corner spines on prefemur of ultimate legs; M, Pore field on coxopleuron (left).

Coxopleural process moderately long with two apical spines (rarely 1 or 3), one subapical spine or none, one to two lateral spines or none, and one dorsal spine or none (Fig. 5I). Coxopleura with dense pore field covering whole area except on ventro-distal part of coxopleural process (Figs. 5J, 6M), pore-free area on coxopleural process extending 50–70% length from distal part to the margin of sternite of ultimate leg-bearing segment (Fig. 5I). Ultimate legs long and slender with ratios of lengths of prefemur and femur 6:4, tibia and tarsus 2 1.5:1; tarsus 1 and tarsus 2 03:2. Prefemoral spines in four rows (Fig. 5K–L), formula VL-4–5 (rarely 2, 6 and 7), VM-3–4 (rarely 1 or 2), M-2–5 (usually 4), DM-1–4 including corner spine (rarely 5 or 6).

Locomotory legs with or without short setae, usually legs 1–5 with two tarsal spurs (rarely 1–2 or up to 6 and 7), the subsequent legs to 21 with one tarsal spur. One tibial spur on legs 1–2 or 3 in equal frequency (rarely 1–4). Leg 1 with femoral spur (rarely absent). Two accessory spurs and pretarsal claw present on all legs. Dorsal part of prefemur of leg 20 with one spine (Fig. 5M, N) at the margin of prefemur (atypically found only on one side). Anterior face of leg 20 in some males with a short, rounded, variably depigmented projection on distal end of tarsus 1 (Fig. 6I); similarly proportioned projection on tarsus 1 of leg 21 in two of four specimens with a projection on leg 20; projections most strongly developed in the largest specimen (Fig. 6J).

Remarks. The taxonomic status of *O. spinosus* and *O. punctiventer* Tömösváry, 1885 is still unclear, the two species possessing the synapomorphic character of a distal prefemoral spine on leg 20. In this study, we found that the range of variation of some taxonomic characters in *O. spinosus* to overlap with the description of *O. punctiventer* sensu Lewis, 2010 (see Table 2). Moreover, the geographic distributions of *O. punctiventer* and *O. spinosus* overlap at least on peninsular Malaysia. For these reasons, the identification based on morphology of *O. spinosus* and *O.punctiventer* is complicated and needs to be reassessed. The nominate subspecies of *O. spinosus* is recognised in this work; *O. spinosus spinosus* Porat, 1876 and *O. spinosus nannus* Chamberlin, 1939 are currently valid subspecies, though the latter has been questioned as possibly being based upon a juvenile specimen of *Ethmostigmus rubripes spinosus* (Newport, 1845) (Schileyko & Stagl, 2004). The type locality of *O. spinosus nannus* is Doormanpad, Irian Jaya/West Papua (New Guinea). We found one specimen of *Otostigmus* in the NHM from Mimika River, Irian Jaya, that we identified as *O. spinosus* but its associated label indicated affinities to *O. punctiventer*.

In Thailand, *O. spinosus* is widespread throughout the southern part of the country (Fig. 1). In all localities this species was found together with other *Otostigmus* species such as *O. multidens*, *O. rugulosus*, *O. astenus*, and *O. scaber*. As some taxonomic characters, such as the range of appearances of tibial and tarsal spurs on the locomotory legs, number of antennal articles, and numbers of apical and lateral spines on the coxopleural process are variable (Table 1), there can be problems in determining species. On some occasions we found animals in which the spine on the prefemur of leg 20, a diagnostic character, was absent on one side. The characteristic of leg 20 (and variably 21) bearing a distal projection on the anterior face of tarsus 1 is apparently unique to this species and, with the data at hand, appears to be a secondary sexual characteristic. The three specimens possessing this feature that exhibit the genital segments are all males and its elaboration with growth is consistent with it being sex-specific. Other Otostigminae have distal processes on different articles of the ultimate leg-pair in males, e.g., on the inner side of the femur in *Digitipes* Attems, 1930, and on the inner side of the tibia in *Otostostigmus* (*Parotostigmus*) *tibialis* Brölemann, 1902. The inconsistency of taxonomic characters may be problematic when it involves the purported diagnostic characters of species and may lead to misidentifications. Molecular data could assist with revaluating species delimitation in the *Otostigmus rugulosus* group (sensu Lewis, 2010).

Variation and development of taxonomic characters. In this study, we found two broods that belong to adolescent stages that permitted investigating the development of some taxonomic characters. In hatchlings in brood D, an early first adolescent stage, most taxonomic characters are incompletely developed. Contrastingly, in the four surviving hatchlings of brood A, some taxonomic characters (including some species-diagnostic characters) are fully developed. Our observations reveal that some traditional taxonomic characters such as number of antennal articles, number of glabrous articles, and number of apical spines on the ultimate leg coxopleuron vary during the life span. A distinguishing character of this species (the prefemoral spine on leg 20) is strongly fixed, being conserved between the mother and second adolescent stage hatchlings except in one specimen (see Table 2) presumably due to abnormal development. Colouration differs between young and the mother; hatchlings show a very light yellowish or brown and magenta colour whereas mothers are dark greenish brown.

DISCUSSION

Otostigmus spinosus exhibits similar hatching and maternal care to other scolopendromorphs. The season in which eggs are laid and brooded varies between different geographic regions, presumably affected by factors such as humidity and temperature. The Neotropical *O. scabricauda* seems to start brooding in early October (Machado, 2000) while *O. spinosus* in Thailand exhibited this behaviour during June–July. In contrast to a debate over whether the mother broods with dorsal or ventral side towards the brood in Geophilomorpha (Bonato & Minelli, 2002; Edgecombe et al., 2010), the position of the mother's body coiling around the cluster of hatchlings is conserved across all families of Scolopendromorpha. The benefit of this brooding posture has been demonstrated in experimental study of *Scolopendra cingulata* Latreille, 1829 (Radl, 1992). That study showed that eggs or hatchlings cannot develop without their mother coiling around them, and survival efficiency of hatchlings decreases when they are separated from the mother.

Table 2. Taxonomic characters of *O. spinosus* from different geographic regions. ? refers to unclear character

Taxonomic Characters	Regional Area of Examined Specimens					
	Burma[1]	**Peninsula Malaysia and Singapore**[2]	**Thailand and Laos**[3]	**Java and Sumatra**[4]	**New Guinea**[5]	***O. punctiventer***[6]
No. of antennal articles	?	20–21	18–24	17–20	20–21	19–22
No. of glabrous articles	?	2.2–2.3	2.2–2.7	2.5	2.2	2–2.3
No. of forcipular teeth	?	3/3 or 4/4	3/3, 4/4, 5/5 or 6/6	4/4	4/3	3/3
Paramedian suture complete from tergite no.	?	5 or 6	5,6 or 7	5	6	5–7
Margination starting from tergite no.	?	7, 9 or 11	9, 10, 11, 13 or 15	9	9	7–9
Sternal paramedian sutures	?	Present (10–20% on anterior)	Present (10–30% on anterior)	Present	Present (20% on anterior)	20–27%
Number of apical spines on coxopleuron	?	1 or 2	1 or 2 (rarely 3)	2–3	2	1–2
Number of lateral spines on coxopleuron	?	1 or absent	1 or 2	1	1	2
Number of dorsal spines on coxopleuron	?	1–2	1	1	1	1
Length of coxopleural process	?	Long	Moderately long	?	Moderately long	Moderately long
Prefemoral spine formula of ultimate leg	?	VL-4 to 5 VM-2 to 3 M-3 to 4 DM-3	VL-2 to 7 VM-2, 3 to 4 M-2 to 5 DM-1 to 6	VL-5 VM-3 DM-5	VL-4 to 5 VM-2 to 3 M-2 to 3 DM-0 to 2	VL- 4 to 5 VM-2 to 3 M-2 to 3 DM-0 to 2
No. of corner spines on prefemoral process of ultimate legs	?	2	1–2	1	1–5	1
Leg No. with 2 tarsal spurs	?	1–2 or 1–4	1, 1–2, 1–3, 1–4, 1–5 or 1–6	?	1–3,4?,5?	1–2
Leg No. with 1 tarsal spur	Reach to 21	3, 5–21	2, 3, 4, 5, 6 or 7–21	?	6–21	?
Femoral and tibial spur on leg no.	?	1 or absent	1–2, 1–3 or only 1	?	1	?
Leg 20 with prefemoral spine	present	present	present	present	?	present

Note: Superscripts refer to cited literature and examined specimen; 1= Pocock, 1891; 2= Verhoeff, 1937; 3= Thai & Laos specimens; 4= Haase, 1887; 5= BMNH collection (1 specimen); 6= Lewis, 2010

Development of embryonic stages in scolopendrids has been described in a few previous works (Heymons, 1901; Lawrence, 1947; Lewis, 1981). In this study, we found stages corresponding to first (brood D) and the second adolescent stages (brood A) and the first (brood F) and third embryonic stages (broods B and E) as described by Lawrence (1947, 1984). The number of segments is fixed at 21 in all studied specimens, conforming to epimorphic development. Bücherl (1971) described the cluster of eggs in *O. tibialis* and *O. scabricauda* numbering 15–30 in each brood, and for *O. scabricauda* Machado (2000) observed a range of 16–58 (mean 29.1) for nine broods. In this study we found 19, 27, 19, 21, 20, and 16 eggs or adolescents in broods A–F, respectively. Body size of adults differs substantially between these three species, with *O. spinosus* having a body length of 38 mm (holotype description 45 mm.), *O. tibialis* 80 mm, and *O. scabricauda* 70 mm (Attems, 1930a; Lewis, 2010). This demonstrates that size of the mother does not appear to influence reproductive efficiency.

Embryonic development has been a focus of developmental biologists studying gene expression during differentiation and growth of centipedes (Brena & Akam, 2012). However, development in taxonomic characters during the life span of these animals still lacks data for many species, although some variation during post-embryonic development has been documented for species of *Otostigmus* and *Scolopendra* by Lewis (1968, 2000). In our study, the results support previous records that some taxonomic characters change during post-embryonic development, among them length of the coxopleural process, number of spines and the arrangement of spines on the coxopleural process, the presence of paramedian sutures on the sternites and tergites, tergite margination, and number of antennal articles. Filial cannibalism has now been confirmed in *O. spinosus* (direct observation of the mother consuming the eggs in brood F, and suggested by the disappearance of hatchlings in brood A in the laboratory), as has been observed in other scolopendromorphs (Brunhuber, 1970; Lawrence, 1984), including *O. scabricauda* (Machado, 2000). This phenomenon has been reported throughout the animal kingdom when parents and their young live together in high selective pressure environments such as high predation, limited feeding and poor environment, which influence survival efficiency of the hatchlings and parent (Klug & Lindstrom, 2008; Chin-Baarstad et al., 2009). Understanding on behaviour and development of scolopendrids contributes to knowledge of their biology and ecology. Moreover it clarifies problems involving variability of morphological characters and thus contributes to an improved classification of the group.

ACKNOWLEDGEMENTS

We would like to thank all members of the Animal Systematics Research Unit and Department of Biology, Faculty of Science, Chulalongkorn University for help during field collecting and for technical support. We thank T. Backeljau for his kindness in finding literature. We would like to express our grateful thanks to the Thai Navy and Army and The Plant Genetic Conservation Project under the Initiative of Her Royal Highness Princess Maha Chakri Sirindhorn for support and permission to collect in some restricted natural reserve areas. We are grateful for financial support from the Thailand Research Fund through the Royal Golden Jubilee PhD Program (Grant No. PHD/0066/2553). The main funding support for this project is from The Thailand Research Fund (TRF) under TRF Senior Research Scholar (RTA 5880001) to SP. We sincerely thank faculty of Science and Graduate school for Oversea Academic Presentation Scholarship. We give special thanks to John Lewis and Varpu Vahtera for their valuable input as referees.

LITERATURE CITED

Attems C (1930a) Myriapoda 2. Scolopendromorpha. In: Schulze FE & Kükenthal W (eds.) Das Tierreich, 54. Walter de Gruyter, Berlin. Pp. 1–308.

Attems C (1930b) Myriopoden der Kleinen Sunda-Inseln, gesammelt von der Expedition Dr. Rensch. Mitteilungen aus dem Zoologischen Museum in Berlin, 16: 117–184.

Bonato L, Edgecombe GD, Lewis JGE, Minelli A, Pereira LA, Shelley RM & Zapparoli M (2010) A common terminology for the external anatomy of centipedes (Chilopoda). ZooKeys, 69: 17–51.

Bonato L & Minelli A (2002) Parental care in *Dicellophilus carniolensis* (C.L. Koch, 1847): new behavioural evidence with implications for the higher phylogeny of centipedes (Chilopoda). Zoologischer Anzeiger, 241: 193–198.

Brena C & Akam M (2012) The embryonic development of the centipede *Strigamia maritima*. Developmental Biology, 363: 290–307.

Brölemann HW (1902) Myriapodes des Musée de São Paolo. Revista do Museu Paulista, 5: 35–237.

Brunhuber BS (1970) Egg laying, maternal care and development of young in the scolopendromorph centipede *Cormocephalus anceps anceps* Porat. Zoological Journal of the Linnean Society, 49: 49–59.

Bücherl W (1971) Venomous chilopods or centipedes. In: Bucherl W (ed.) Venomous Animals and their Venoms. Volume 3, Venomous Invertebrates. Academic Press, New York. Pp. 167–196.

Chao J-L (2008) Scolopendromorpha (Chilopoda) of Taiwan. Collection, Description, Illustration, Taxonomy, Distribution. VDM Verlag Dr. Müller, Saarbrücken, 94 pp.

Chamberlin RV (1939) On a collection of chilopods from the East Indies. Bulletin of the University of Utah, 29 (Biological Series 15): 1–19.

Chamberlin RV (1944) Some chilopods from the Indo-Australian Archipelago. Notulae Naturae, 147: 1–14.

Chin-Baarstad A, Klug H & Lindstrom K (2009) Should you eat your offspring before someone else does? Effect of an egg predator on filial cannibalism in the sand goby. Animal Behaviour, 78: 203–208.

Edgecombe GD & Giribet G (2007) Evolutionary biology of centipedes (Myriapoda: Chilopoda). Annual Reviews of Entomology, 52: 70–151.

Edgecombe GD, Bonato L & Giribet G (2010) Brooding in *Mecistocephalus togensis* (Geophilomorpha: Placodesmata) and the evolution of parental care in centipedes (Chilopoda). International Journal of Myriapodology, 3: 139–144.

Haase, E (1887) Die Indisch-Australischen Myriopoden. 1. Chilopoden. Abhandlungen und Berichte des Königlichen zoologischen und antrhropologisch-ethnographischen Museum zu Dresden, 4, 5: 1–118.

Heymons R (1901) Die Entwicklungsgeschichte der Scolopender. Zoologica, 13: 1–244.

Humbert A & de Saussure H (1870) Myriapoda nova Americana, Series 2. Revue et Magasin de Zoologie, 22: 196–220.

Khanna V (1994) Centipede fauna of NE States, India (Chilopoda: Scolopendromorpha). Records of the Zoological Survey of India, 94: 459–472.

Khanna V (2001) A check-list of the Indian species of the centipedes (Chilopoda: Scolopendromorpha). Annals of Forestry, 9: 199–219.

Klug H & Lindstrom H (2008) Hurry-up and hatch: selective filial cannibalism of slower developing eggs. Biology Letters, 4: 160–162.

Kraepelin K (1903) Revision der Scolopendriden. Jahrbuch der Hamburgischen wissenschaftlichen Anstalten, 20(2): 1–276.

Kraepelin K (1904) Catalogue des Scolopendrides des collections du Muséum d'Histoire Naturelle de Paris (Collection du Muséum determinée par M. Le Professor Karl Kraepelin, et collection H. W. Brölemman). Bulletin de Muséum d'Histore naturelle Paris, 1904: 243–253, 316–325.

Lawrence RF (1947). Some observations on the post-embryonic development of the Natal forest centipede, *Cormocephalus multispinus* (Kraep.). Annals of the Natal Museum, 11: 139–156.

Lawrence, RF (1984) The Centipedes and Millipedes of Southern Africa: A Guide. Taylor & Francis, Rotterdam, Cape Town, 148 pp.

Leach WE (1813–1815) A tabular view of the external characters of four classes of animals, which Linné arranged under Insecta; with the distribution of the genera composing three of these classes into orders, & and descriptions of several new genera. Transactions of the Linnean Society of London, 11: 306–400.

Lewis JGE (1968) The variation of the centipede *Scolopendra amazonica* in Africa. Zoological Journal of the Linnean Society, 48: 49–57.

Lewis JGE (1978) Variation in tropical scolopendrid centipede: problems for the taxonomist. Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg, 21: 51–54.

Lewis JGE (1981) The Biology of Centipedes. Cambridge University Press, Cambridge, UK, 476 pp.

Lewis JGE (1982). The scolopendrid centipedes of the Oxford University 1932 Sarawak Expedition. Journal of Natural History, 16: 389–397.

Lewis JGE (1984) The Myriapoda of the Gunung Mulu National Park. The Sarawak Museum Journal, 30: 35–51.

Lewis JGE (1991) Scolopendromorph and geophilomorph centipedes from the Karakatau Islands and adjacent regions, Indonesia. Memoirs of the Museum of Victoria, 52: 337–353.

Lewis JGE (2000) Variation in three centipede species of the genus *Otostigmus* and its bearing on species discrimination (Chilopoda; Scolopendromorpha; Scolopendridae), Journal of Natural History, 34: 433–448.

Lewis JGE (2001). The scolopendrid centipedes in the collection of the National Museum of Natural History in Sofia (Chilopoda: Scolopendromorpha: Scolopendridae). Historia Naturalis Bulgarica, 13: 5–51.

Lewis JGE (2010) A revision of the *rugulosus* group of *Otostigmus* subgenus *Otostigmus* Porat, 1876 (Chilopoda: Scolopendromorpha: Scolopendridae). Zootaxa, 2579: 1–29.

Linnaeus C (1758) Systema Naturae. Editio Decima. Laur. Salvius, Holmiae, 824 pp.

Machado G (2000) Maternal care in the neotropical centipede *Otosigmus scabricauda* (Chilopoda: Scolopendromorpha). Entomological News, 111: 250–254

Minelli A, Bonato L, Dioguardi R, Chagas-Júnior A, Edgecombe GD, Lewis JGE, Pereira LA, Shelley RM, Stoev P, Uliana M & Zapparoli M (2006) Chilobase: a Web Resource for Chilopoda Taxonomy. http://chilobase.bio.unipd.it (Accessed 31 January 2014)

Mitić BM, Antić DŽ, Ilic BS, Makarov SE, Lučić LR & Ćurčić BPM (2012) Parental care in *Cryptops hortensis* (Donovan) (Chilopoda: Scolopendromorpha) from Serbia, the Balkan Peninsula. Archives of Biological Sciences, Belgrade, 64: 1117–1121.

Newport G (1844) [Conclusion of the monograph on the Myriapoda Chilopoda]. Proceedings of the Linnean Society of London, 1: 191–197.

Newport G (1845) Monograph of the class Myriapoda order Chilopoda; with observations on the general arrangement of the Articulata. Transactions of the Linnean Society of London, 19: 265–302, 349–439.

Pocock RI (1891a) Notes on the synonymy of some species of Scolopendridae, with descriptions of new genera and species of the group. Annals and Magazine of Natural History, Series 6, 7: 51–68, 221–231.

Pocock RI (1891b) On the Myriopoda of Burma. Part 2. Report upon the Chilopoda collected by Sig. L. Fea and Mr. E. W. Oates. Annali del Museo Civico di Storia Naturale Giacomo Doria, Genova, 30: 401–432.

Pocock RI (1894) Chilopoda, Symphyla and Diplopoda from the Malay Archipelago. In: Weber M (ed.) Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien, Volume 3. Brill, Leiden 307–404.

von Porat C (1876). Om några exotiska myriopoder. Bihang till Kongliga Svenska Vetenskaps-Akademien Handlingar, 4, 7: 1–48.

Radl RC (1992). Brood care in *Scolopendra cingulata* Latreille (Chilopoda: Scolopendromorpha). Naturwissenschaftlich-medizinischer Vereins in Innsbruck, Supplement, 10: 123–127.

Schileyko AA (2007) The scolopendromorph centipedes (Chilopoda) of Vietnam, with contributions to the faunas of Cambodia and Laos. Part 3. Arthropoda Selecta, 16: 71–95.

Schileyko AA & Stagl V (2004) The collection of scolopendromorph centipedes (Chilopoda) in the Natural History Museum in Vienna: a critical re-evaluation of former taxonomic identifications. Annalen des Naturhistorisches Museum Wien, 105: 67–137.

Tömösváry E (1885) Myriopoda a Joanne Xanthus in Asia Orientali collecta. Természatrajzi Füzetek, 6: 63–72.

Verhoeff KW (1937) Chilopoden aus Malacca, nach den Objecten des Raffles Museum in Singapore. Bulletin of the Raffles Museum, 13: 198–270.

Wood HC (1862) On the Chilopoda of North America, with a catalogue of all the specimens in the collections of the Smithsonian Institution. Journal of the Academy of Natural Sciences, Philadelphia, Series 2, 5: 2–52.

Zeh DW & Smith RL (1985) Parental investment by terrestrial arthropods. American Zoologist, 25: 785–805.