

# Reinstatement of *Dermacentor bellulus* (Acari: Ixodidae) as a Valid Species Previously Confused with *D. taiwanensis* and Comparison of All Parasitic Stages

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**ABSTRACT** Re-examination of *Dermacentor taiwanensis* Sugimoto, 1935 specimens in the United States National Tick Collection revealed that two morphologically distinct *Dermacentor* species were identified under this name. One of them corresponds to Sugimoto's description of *D. taiwanensis*, while another species is identical to Schulze's *Dermacentor bellulus* (Schulze, 1935). The latter species has not been considered valid by recent workers. *D. bellulus* is reinstated here as a valid species and all its stages are redescribed. The adults of *D. taiwanensis* are also redescribed, and its immature stages are described for the first time. Males and females of *D. bellulus* can be distinguished from those of *D. taiwanensis* by the shape of the conscutum and scutum, color pattern, genital structures, size of the palpi and cornua, and the spurs of coxa I. Nymphs of *D. bellulus* can be distinguished from those of *D. taiwanensis* by the shape of the scutum, basis capituli, and the hypostomal dentition. Larvae of *D. bellulus* can be differentiated from those of *D. taiwanensis* by the shape of the basis capituli, and the degree of development of the auriculae and spur on palpal segment III ventrally. *D. bellulus* has been recorded from China, Japan, Nepal, Taiwan, and Vietnam; adults have been collected from wild boars, bears, panda, dog, and human; the immature stages are known from rodents, hares, ferret-badger, and bamboo-partridge. *D. taiwanensis* is found in China, Taiwan, and Vietnam; adults have been collected from wild boars; the immature stages are known from rodents, hares, mustelids, and domestic dog.

**KEY WORDS** *Dermacentor bellulus*, *Dermacentor taiwanensis*, description

Ticks of the genus *Dermacentor* Koch, 1844 that occur chiefly in the Oriental zoogeographic region comprise a compact and apparently natural group, designated subgenus *Indocentor* Schulze, 1933. Currently, six *Indocentor* species are generally recognized: *D. atrosignatus* Neumann, 1906, *D. auratus* Supino, 1897, *D. compactus* Neumann, 1901, *D. confragus* (Schulze, 1933), *D. steini* (Schulze, 1933), and *D. taiwanensis* Sugimoto, 1935. The systematics of subgenus *Indocentor* was largely developed by Schulze (1933, 1935) and revised in a series of papers by Wassef and Hoogstraal (1983; 1984a,b; 1986a,b). Nevertheless, *Indocentor* species remain little studied and poorly known, possibly because all active life history stages parasitize wild animals, mostly mammals, in the primary forests of South and Southeast Asia.

During re-examination of supposed *D. taiwanensis* specimens in the United States National Tick Collection (USNTC), two morphologically distinct *Dermacentor* species were found. Both had been identified as

*D. taiwanensis* by previous workers. Comparison of these specimens with other described *Dermacentor* taxa revealed that they are identical to two species described from Taiwan, namely *D. taiwanensis* and *D. bellulus* (Schulze, 1935). The latter name has not been recognized as valid in all recent lists (Guglielmo et al. 2010, 2014) and was synonymized with *D. atrosignatus* (Sugimoto 1937, Estrada-Peña 1991), *D. auratus* (Teng and Jiang 1991), or *D. taiwanensis* (Camicas et al. 1998, Sun and Xu 2013) or considered *incertae cedis* in Guglielmo and Nava (2014). The presence of a number of distinctive diagnostic characters in the male, female, nymph, and larva persuaded us to reinstate *D. bellulus* as a valid species and redescribe all its parasitic stages. For comparative purposes, we also redescribe the male and female of true *D. taiwanensis* and describe its nymph and larva for the first time.

## Materials and Methods

The material examined is summarized in Tables 1 and 2. Field-collected and laboratory-reared ticks were available for study. The specimens that were examined are deposited in the USNTC (Georgia Southern University, Statesboro), Institute of Zoology of the Chinese

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Table 1. *Dermaecentor bellulus*, material examined

♂	♀	No. of ticks <sup>a</sup>			Host	Locality; altitude (m)	Date	Collector <sup>b</sup>	Accession no. <sup>c</sup>
		♀	N	L					
China									
4					Sus scrofa	Fujian, Nanping County			D-048-05
1					Ursus sp.	Fujian, Shaowu County	DW		D-048-01
1	1				Alaropoda melanoleuca	Sichuan, Tianquan County	WQ		D-047-11
1					Ursus thibetanus	Xizang, Medog County, Gutang; 2400			D 300
Japan									
1					Sus scrofa	Fukui, Shizuhara	JA		00714209
2						Kagoshima, Yunwan-dake	VT		00714173
2					Sus scrofa	Kagoshima, Uken			00714408
4	2				Sus scrofa	Kagoshima, Uken			00714692
	1				Sus scrofa	Kagoshima, Uken			00714613
4 <sup>d</sup>	2 <sup>d</sup>	2;5 <sup>d,e</sup>	7;5 <sup>d</sup>		Vegetation <sup>f</sup>	Kanagawa, Kuribana & Kyoto, Mineyama <sup>f</sup>	YS		00714414
1					Sus scrofa	Kyoto, Kyoto			00714289
					Apodemus spectosus	Kyoto, Ohara			00714535
Nepal									
1					Vegetation	Nuwakot, Syahrn; 1829	RMM		00714845
					Vegetation	Rasuwa, Syaaurbensii; 1448	RMM		00714917
Taiwan									
		7	47		Bandicota indica	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714185
		2 <sup>d</sup>	2 <sup>e</sup>		Bandicota indica	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714509
		1	1		Mus caroli	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714423
2 <sup>d</sup>	4 <sup>d</sup>	1 <sup>e</sup>	1 <sup>e</sup>		Niviventer coninga	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714798
	1 <sup>d</sup>	1 <sup>e</sup>	1 <sup>e</sup>		Niviventer coninga	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714800
		1 <sup>e</sup>	1 <sup>e</sup>		Niviventer coninga	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714609
		1 <sup>e</sup>	1 <sup>e</sup>		Niviventer coninga	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714531
		1 <sup>e</sup>	1 <sup>e</sup>		Niviventer coninga	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714204
		2	2		Rattus losea	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714085
		1	1		Rattus losea	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714571
		2 <sup>d</sup>	1 <sup>e</sup>		Rattus losea	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714135
		1	1		Rattus losea	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714938
		1 <sup>e</sup>	1 <sup>e</sup>		Rattus losea	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714586
		1 <sup>e</sup>	1 <sup>e</sup>		Rattus losea	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714840
		2	2		Rattus losea	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714153
		1 <sup>e</sup>	1 <sup>e</sup>		Rattus losea	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714556
1 <sup>d</sup>		1 <sup>e</sup>	1 <sup>e</sup>		Bandicota indica	Taipei, San-chih, Ch'e-ch'eng; 376	FJS		00714807
		1 <sup>e</sup>	1 <sup>e</sup>		Rattus losea or Niviventer coninga	Taipei, San-chih, Ch'e-ch'eng or Shu-hsing Li, Hsing-fu-liao; 332	FJS		00714904
		2	5;3 <sup>e</sup>		Melagale moschata	Taipei, Ta-t'un Shan, Pai-lin-chia	FJS		00714354
		7	5;3 <sup>e</sup>		Lepus sinensis	Taipei, Ta-t'un Shan, Pai-lin-chia; 594-891	FJS		00714074
		2	2		Bandicota indica	Taipei, Ta-t'un Shan, Pai-lin-chia; 693	FJS		00714932
		1 <sup>e</sup>	1 <sup>e</sup>		Bandicota indica	Taipei, Ta-t'un Shan, Pai-lin-chia; 693	FJS		00714700
		1 <sup>e</sup>	1 <sup>e</sup>		Bandicota indica	Taipei, Ta-t'un Shan, Pai-lin-chia; 693	FJS		00714697
		1	1		Bambusicola thoracica	Taipei, Ta-t'un Shan, Pai-lin-chia or San-chih, Ch'e-ch'eng; 376	FJS		00714582

(Continued)

Table 1. Continued

♂	♀	No. of ticks <sup>a</sup>		Host	Locality; altitude (m)	Date	Collector <sup>b</sup>	Accession no. <sup>c</sup>
		N	L					
3	2			<i>Sus scrofa</i>	Taipei, Tan-shui, Pai-lin-chia-ting	5.II.1975	FJS	00714171
				<i>Lepus sinensis</i>	Taipei, Tan-shui, Pai-lin-chia-ting; 500	15.II.1973	FJS	00714576
				<i>Lepus sinensis</i>	Taipei, Tan-shui, Pai-lin-chia-ting; 500	21.II.1973	FJS	00714640
8	2			<i>Sus scrofa</i>	Taipei, Wu-lai	25.II.1959	REK	00714335
2	2			<i>Sus scrofa</i>	Taipei, Yang-ming-shan	17.XI.1961	REK	00714335
1	1			<i>Sus scrofa</i>	Taipei, Yang-ming-shan	17.XI.1961	REK	00714077
1				<i>Sus scrofa</i>	Taito	18.X.1936		00714962
16	3			<i>Sus scrofa</i>	Taitung, Pei-yuan; 198	10 or 18.XI.1971	CJC	00714904
2	3			<i>Sus scrofa</i>	Taitung, Pei-yuan; 300	11 or 14.II.1971	CJC	00714425
2	1			<i>Sus scrofa</i>	Taitung, Pei-yuan; 300	14.II.1971	CJC	00714659
11				<i>Sus scrofa</i>	Taitung, Pei-yuan, Shih-nan; 198	10.XI.1970	CJC	00714604
10	3			<i>Sus scrofa</i>	Taitung, Pei-yuan, Shih-nan; 198	10.I.1972 or 10.I.1973	FJS	00714747
4	1			<i>Sus scrofa</i>	Taitung, Pei-yuan, Shih-nan; 198	10.I.1973	FJS	00714735
3	1			<i>Sus scrofa</i>	Taitung, Pei-yuan or Tung-ho	5 or 11.II.1971	CJC	00714168
				<i>Sus scrofa</i>	Taitung, Tung-ho	11.I.1972	CJC	00714768
2	1			<i>Sus scrofa</i>	Taitung, Tung-ho, Pei-yuan	15.XI.1965	SYL	00714291
1	1			<i>Sus scrofa</i>	Taitung, Tung-ho, Pei-yuan	4.V.1970	JCL	00714066
18	1			<i>Sus scrofa</i>	Taitung, Tung-ho or Pei-yuan; 300	5.II. or 12.IX.1970	CJC	00714839
				<i>Sus scrofa</i>	Tosei	1955	S	00714922
				No data		10.III.1974	FJS	00714847
Vietnam								
				<i>Rattus tanezumi</i>	Da Nang, Da Nang; 10	1.V.1966	FJS	00860989
3	5			<i>Rattus norvegicus</i>	Da Nang, Da Nang	11.VIII.1969	RHG	00860986
				<i>Rattus</i> sp.	Da Nang, Mt. Sontra; 594	7.IX.1967	PFDVP	00714147
1	1			<i>Rattus tanezumi</i>	Da Nang, Mt. Sontra; 164	20.IV.1966	FJS	00714969
				<i>Rattus</i> sp.	Da Nang, Mt. Sontra; 446	12.VIII.1967	PFDVP	00860991
1	3			<i>Rattus</i> sp.	Da Nang, Mt. Sontra; 594	7.IX.1967	PFDVP	00860997
				<i>Rattus rattus</i>	Da Nang, Mt. Sontra; 396	11.VIII.1967	GSJ	00860990
1	1			<i>Rattus rattus</i>	Da Nang, Mt. Sontra; 425	4.X.1967	GSJ	00860988
1	1			<i>Rattus rattus</i>	Da Nang, Mt. Sontra; 97	IV.1969	PFDVP	00860992
2	2			<i>Rattus</i> sp.	Da Nang, Mt. Sontra; 10	8.VIII.1967	PFDVP	00860995
				Rats	Da Nang, Sontra	V.VI.1989	VS	Tdi
				<i>Tupaia glis</i>	Da Nang, Sontra	4.VI.1989		Tdi
1	1			<i>Rattus rattus</i>	Da Nang, Sontra	9.VI.1989	VS	Tdi
127				Rats	Da Nang, Sontra	V.VI.1989		Tdi
50				Rodents	Da Nang, Sontra	VII-VIII.1989	VS	Tdi
2	2			<i>Rattus rattus</i>	Da Nang, Sontra; 629	19.VII.1989		Tdi
1				Clothing	Dak Lak, Krong Knmar, Chu Yang Sin National Park; 950	V.2014	AVA	ZIN
4	4			<i>Rattus rattus</i>	Dong Nai, Ma Da	17.I.1994	SS	Tdi
				<i>Bandicota bengalensis</i>	Dong Nai, Ma Da	4.III.1991	VS	Tdi
				<i>Niviventer</i> sp.	Lam Dong, Da Lat	7.XII.1995	VS	Tdi
1	1			<i>Niviventer</i> sp.	Lam Dong, Da Lat	6.XII.1995	GK	Tdi
				Rodents	Lam Dong, Da Lat	XII.1995	GK, VS	Tdi
2	2			<i>Niviventer</i> sp.	Lam Dong, Da Lat, Cong-Troi pass	4.XII.1995		Tdi
2	2			<i>Niviventer</i> sp.	Lam Dong, Da Lat, Cong-Troi pass	7.XII.1995	VS	Tdi

(Continued)

Table 1. Continued

♂	♀	No. of ticks <sup>a</sup>		Host	Locality; altitude (m)	Date	Collector <sup>b</sup>	Accession no. <sup>c</sup>
		N	L					
1				<i>Niventer</i> sp. clothing	Lam Dong, Da Lat, Cong-Troi pass	2.XII.1995	GK	Tdi
1				<i>N. confucianus</i>	Lam Dong, Loc Bao, 35 km NW of Loc Bao Town; 650	IV.2012	AVA	ZIN
1					Lao Cai, Hoang Lien Son, Chapa		NMT, VVB	Tdi
1	1			Human	Lao Cai, Van Ban	8.IV.2005	K	Tdi-1965
1				<i>Rattus rattus</i>	Quang Binh, Tuyen-Hoa	1.V.1999	GVK	Tdi-4710
112	36	93	301	Total	Quang Tri, Mt. Thon Ke Tri; 10	26.III.1969	PFDVP	00860985

<sup>a</sup> L, larvae; N, nymphs.

<sup>b</sup> AVA, A.V. Abramov; CIC, C.I. Cheng; DW, D. Wang; FJS, F.J. Santiana; GSJ, G.S. Jones; GVK, G.V. Kuznetsov; JA, J. Akiyama; JCL, J.C. Lien; K, Kalyakin; NMT, Nguyen Minh Tam; PFDVP, P.F.D. Van Peden; REK, R.E. Kuntz; RHC, R.H. Crothaus; RMM, R.M. Mitchell; S, Shilova; SYL, S.Y. Lin; VS, V. Smitzov; SS, S. Shilova; SYL, S.Y. Lin; VS, V. Smitzov; VVB, V.V. Bobrov; WQ, W. Qui; YS, Y. Saito.

<sup>c</sup> USNMMENT number is given for USNTC collection unless specified: D—IZAS; Tdi—ZMMMO; ZIN—ZIAC.

<sup>d</sup> Reared specimen.

<sup>e</sup> Molting skin.

<sup>f</sup> Place where parent larvae were collected.

<sup>g</sup> Here and below "or" in the columns Host, Locality, and Date indicates that the data on the label and in the Harry Hoogstraal Tick Collection catalogue for this collection do not agree; data presented as follows: label data or Harry Hoogstraal Tick Collection catalogue data.

Academy of Sciences (IZAS; Beijing, China), Zoological Museum of Moscow State University (ZMMO; Moscow, Russia), and Zoological Institute of the Russian Academy of Sciences (ZIAC; St. Petersburg, Russia).

The immature stages were mounted on glass slides and examined under a light microscope (Olympus BX41, Olympus Corporation, Tokyo, Japan). All stages were also studied by means of a stereoscopic microscope (Olympus SZX16, Olympus Corporation, Tokyo, Japan) and a scanning electron microscope (JOEL JSM6610LV, JOEL Ltd., Tokyo, Japan). Measurements for the male and female are given in millimeters and those for the various features of the nymph and larva in micrometers. The measurements are arranged as follows: minimum–maximum (mean  $\pm$  SD,  $n$  = number of specimens measured). The nomenclature of larval setae is that of Clifford and Anastos (1960). Host nomenclature is that of Wilson and Reeder (2005). Illustrations presented in figures 1 and 8 have been drawn by D.A. Apanaskevich and colored by M.A. Apanaskevich.

### *Dermacentor bellulus* (Schulze, 1935)

(Figs. 1–6)

**Male.** (redescription) (Figs. 1A, 2, and 3). Conscutum (Figs. 1A and 2): broadly oval with moderately convex lateral margins, widest at posterior third of conscutal length; distance from scapular apices to posterior margin of conscutum 3.69–6.12 ( $4.99 \pm 0.54$ ;  $n = 112$ ), maximum width 2.69–4.50 ( $3.59 \pm 0.41$ ;  $n = 112$ ), ratio length to width 1.31–1.51 ( $1.39 \pm 0.04$ ;  $n = 112$ ). Coloration as illustrated: pale ivory-colored ornamentation moderate to extensive, light- to dark-brown background forms several patches, often with indistinct hazy margins; a pair of narrow cervical patches extending from cervical pits to posterior margin of pseudoscutum; a pair of small patches lateral to cervical patches; broad and hazy central patch on pseudoscutum; posteromedian margin of pseudoscutum indicated by narrow hazy strip; lateral field with two brown patches: anterior broad patch extending medially to lateral grooves from eyes to midlength and posterior narrow patch (often poorly defined or rarely indistinct) along most of lateral margins of conscutum; two pairs of oval patches medial to lateral groove; a pair of central patches; narrow stripes in posteromedian and paramedian regions; first and second festoons mostly ivory colored, third and fourth festoons mostly brown, paramedian and median festoons with large ivory spots; all punctations from whitish- to dark-brown. In lighter or darker colored specimens (Fig. 2A–D) some patches may become indistinct or oppositely fused together. Central field posterior to pseudoscutum often flat, imparting a concave appearance to conscutum; conscutum smooth. Cervical grooves shallow; a pair of central slight depressions, and a second posterior pair of slight depressions that correspond to paramedian grooves; lateral grooves distinct, extending from just posterior to eyes to first festoons and aligned with large punctations; 11 distinct festoons, median festoon usually as broad as paramedian festoons. Very large and deep punctations moderately dense, distributed over entire conscutum but

Table 2. *Dermacentor taiwanensis*, material examined

♂	No. of ticks <sup>a</sup>			Host	Locality, altitude (m)	Date	Collector <sup>b</sup>	Accession no. <sup>c</sup>
	♀	N	L					
China	1				Hainan, Jianfengling	IV.1980		D-047-14
Taiwan								
1 <sup>d</sup>	1 <sup>d</sup>			<i>Bandicota indica</i>	Taipei, Hou Shan or <sup>e</sup> Shu-hsing Li, Hsing-fu-liao; 323	30.VI.1972	FJS	00714971
1 <sup>d</sup>	1 <sup>d</sup>			<i>Bandicota indica</i>	Taipei, San-chih, Ch'e-ch' eng; 376	11.V.1973	FJS	00714584
				<i>Bandicota indica</i>	Taipei, San-chih, Ch'e-ch' eng; 376	11.V.1973	FJS	00714084
				<i>Bandicota indica</i>	Taipei, San-chih, Ch'e-ch' eng; 376	11.V.1973	FJS	00714083
				<i>Bandicota indica</i>	Taipei, San-chih, Ch'e-ch' eng; 376	11.V.1973	FJS	00714402
				<i>Bandicota indica</i>	Taipei, San-chih, Ch'e-ch' eng; 376	11.V.1973	FJS	00714633
				<i>Bandicota indica</i>	Taipei, San-chih, Ch'e-ch' eng; 376	11.V.1973	FJS	00714734
			6	<i>Bandicota indica</i>	Taipei, San-chih, Ch'e-ch' eng; 376	11.V.1973	FJS	00714961
	1 <sup>d</sup>			<i>Bandicota indica</i>	Taipei, San-chih, Ch'e-ch' eng; 475	7.VIII.1974	FJS	00714293
	1 <sup>d</sup>			<i>Bandicota indica</i>	Taipei, San-chih, Ch'e-ch' eng; 475	4.IX.1974	FJS	00714264
				<i>Bandicota indica</i>	Taipei, Shu-hsing Li, Hsing-fu-liao; 323	7.VII.1972	FJS	00714318
			1	<i>Bandicota indica</i>	Taipei, Shu-hsing Li, Hsing-fu-liao; 320	10 or 20.IX.1972	FJS	00714480
	1			<i>Bandicota indica</i>	Taipei, Shu-hsing Li, Hsing-fu-liao, Tan-Shui; 320	10.VII.1972	FJS	00714176
	14			<i>Bandicota indica</i>	Taipei, Shu-hsing Li, Hsing-fu-liao, Tan-shui; 320	30.VI.1972	FJS	00714976
3	1			<i>Sus scrofa</i>	Taipei, Tan-shui, Pai-lin-chia	5.II.1975	FJS	00714110
1 <sup>d</sup>				<i>Calloscturus erythraeus</i>	Taipei, Ta-t'un Shan, Pia-lin-chia; 594-891	30.VIII.1973	FJS	00714548
4 <sup>d</sup>				<i>Lepus sinensis</i>	Taipei, Ta-t'un Shan, Pai-lin-chia; 594-891	23.VII.1973	FJS	00714903
			1,2 <sup>f</sup>	<i>Lepus sinensis</i>	Taipei, Ta-t'un Shan, Pai-lin-chia; 594-891	26.VII.1973	FJS	00714376
			1	<i>Melogale moschata</i>	Taipei, Ta-t'un Shan, Pai-lin-chia; 594-891	9.VIII.1973	FJS	00714813
			1	<i>Melogale moschata</i>	Taipei, Ta-t'un Shan, Pai-lin-chia; 594-891	30.VIII.1973	FJS	00714925
			1 <sup>f</sup>	<i>Melogale moschata</i>	Taipei, Ta-t'un Shan, Pia-lin-chia; 596-891	6.IX.1973	FJS	00714466
			9 <sup>f</sup>	<i>Mustela sibirica</i>	Taipei, Ta-t'un Shan, Pia-lin-chia; 594-891	24.VII.1973	FJS	00714433
			1 <sup>f</sup>	<i>Bandicota indica</i>	Taipei, Ta-t'un Shan, Pai-lin-chia; 693	2.V.1973	FJS	00714564
			1	<i>Melogale moschata</i>	Taipei, Ta-t'un Shan, Pai-lin-chia; 693	11.V. or 19.VII.1973	FJS	00714089
			1	<i>Melogale moschata</i>	Taipei, Ta-t'un Shan, Pai-lin-chia; 693	11.V. or 19.VII.1973	FJS	00714399
10				<i>Melogale moschata</i>	Taipei, Wu-lai	25.II.1959	REK	00714486
1	1			<i>Sus scrofa</i>	Taipei, Yang-ming-shan	17.XI.1961	REK	00714352
2	2			<i>Sus scrofa</i>	Taipei, Yang-ming-shan	17.XI.1961	REK	00714213
	1			<i>Sus scrofa</i>	Taito	18.X.1936		00714490
5	5			<i>Sus scrofa</i>	Taitung, Pei-yuan; 198	10 or 18.XI.1971	CIC	00714302
6				<i>Sus scrofa</i>	Taitung, Pei-yuan; 300	14.II.1971	CIC	00714776
1	1			<i>Sus scrofa</i>	Taitung, Pei-yuan; 300	11 or 14.II.1971	CIC	00714835
1	1			<i>Sus scrofa</i>	Taitung, Pei-yuan, Shih-nan	10.XII.1970	CIC	Tdh-5079
2				<i>Sus scrofa</i>	Taitung, Pei-yuan, Shih-nan; 198	10.XII.1970	CIC	00714501
5	2			<i>Sus scrofa</i>	Taitung, Pei-yuan, Shih-nan; 198	10.I.1972 or 10.I.1973	FJS	00714182
	1			<i>Sus scrofa</i>	Taitung, Pei-yuan or Tung-ho; 300	4 or 12.IX.1970	CIC	00714597
	1			<i>Sus scrofa</i>	Taitung, Tung-ho	11.I.1972	CIC	00714488
7				<i>Sus scrofa</i>	Taitung, Tung-ho or Pei-yuan; 300	5.II. or 12.IX.1970	CIC	00714026
1				<i>Sus scrofa</i>	Taitung, Tung-ho, Pei-yuan	15.XI.1965	SYL	00714186

(Continued)

Table 2. Continued

♂	No. of ticks <sup>a</sup>			Host	Locality; altitude (m)	Date	Collector <sup>b</sup>	Accession no. <sup>c</sup>
	♀	N	L					
Vietnam								
3			1	Vegetation <i>Calloscurtus erythraeus</i>	Bac Thai	29.VI.1985		Tdi
	23			<i>Calloscurtus erythraeus</i>	Bac Thai	29.VI.1985		Tdi
	1			<i>Tamopsis nicellandti</i>	Bac Thai	27.VI.1985	GVK	Tdi
	1			Domestic dog	Bac Thai	27.VI.-2.VII.1985		Tdi
1				Vegetation	Hanoi, Khoshon-Bin, Mai-Choo	31.X.-4.XI.1990	EPN	ZIN 5721
	1			<i>Rattus</i> sp.	Vinh Phuc, Tam Dao	V.1997	NLO	Tdi
51	23	80	12	Total				

<sup>a</sup> L, larvae; N, nymphs.

<sup>b</sup> G/C, C.I. Cheng; EPN, E.P. Narehuk; FJS, F.J. Santana; GVK, G.V. Kolonin; HH, H. Hoogstraal; L, Lowery; M, Muschinske; NLO, N.L. Orlov; REK, R.E. Kuntz; SYL, S.Y. Lin; VS, V. Sunitzov.

<sup>c</sup> USNMNT number is given for USNTC collections unless specified: D—IZAS; Tdi—ZMMO; ZIN—ZIAC.

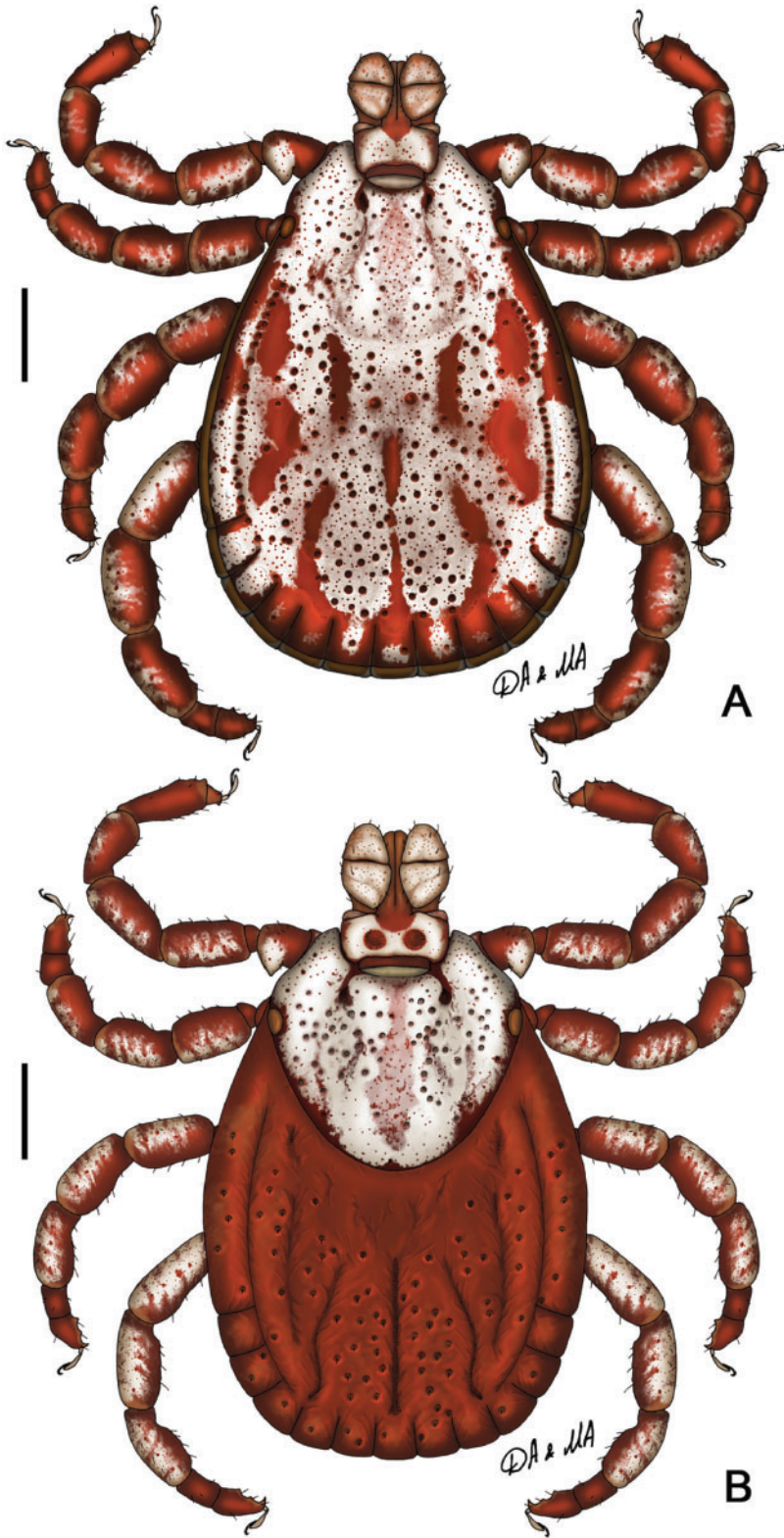
<sup>d</sup> Reared specimen.

<sup>e</sup> Here and below "or" in the columns Host, Locality, and Date indicates that the data on the label and in the Harry Hoogstraal Tick Collection catalogue for this collection do not agree; data presented as follows: label data or Harry Hoogstraal Tick Collection catalogue data.

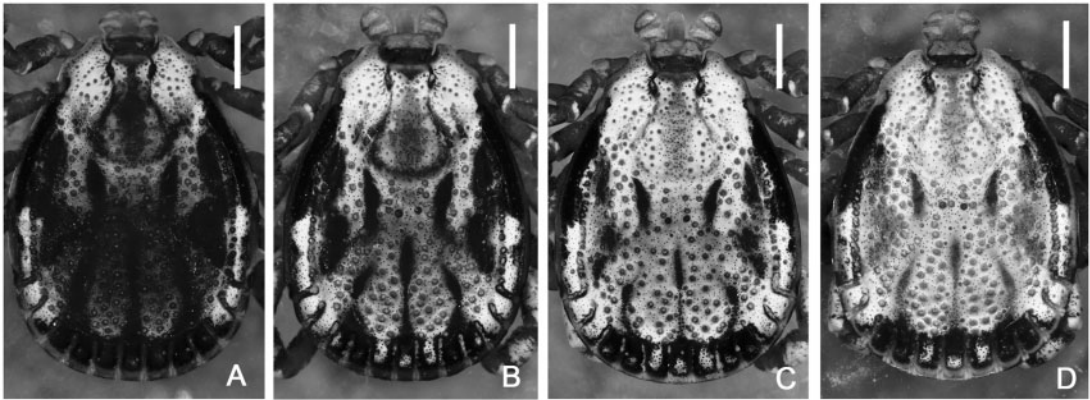
<sup>f</sup> Moulting skin.

denser laterally and posteriorly; large punctations on pseudoscutum rather sparse; fine punctations dense, evenly distributed. Eyes oval, very slightly convex, at anterior one-fifth of conscutal length. Setae relatively short and inconspicuous. Spiracular plates (Fig. 3A): suboval; dorsal prolongation moderately long and broad, with narrow, unperforated widening anteriorly; perforations very small and fairly numerous. Sclerotized plaques on festoons ventrally inornate or with small ivory-colored spot. Gnathosoma (Figs. 1A, 3B and C): length from palpal apices to cornual apices dorsally 0.92–1.46 ( $1.15 \pm 0.10$ ;  $n = 112$ ), width of basis capituli 0.60–0.97 ( $0.79 \pm 0.07$ ;  $n = 113$ ), ratio length to width 1.32–1.57 ( $1.46 \pm 0.05$ ;  $n = 112$ ). Basis capituli (Figs. 1A, 3B and C): dorsally subrectangular; posterior margin nearly straight or slightly concave; length 0.38–0.60 ( $0.49 \pm 0.05$ ;  $n = 112$ ), ratio width to length 1.47–2.00 ( $1.61 \pm 0.08$ ;  $n = 112$ ); cornua broad, short, total length of basis capituli, including cornua, 3.67–8.60 ( $5.01 \pm 0.80$ ;  $n = 112$ ) cornual length; dorsally with extensive whitish enameling. Basis capituli ventrally subrectangular; posterior margin convex. Palpi (Figs. 1A, 3B and C): short, broad; length dorsally (segments I–III) 0.54–0.87 ( $0.67 \pm 0.06$ ;  $n = 113$ ), width 0.32–0.51 ( $0.42 \pm 0.04$ ;  $n = 113$ ), ratio length to width 1.41–1.96 ( $1.60 \pm 0.09$ ;  $n = 113$ ), length of segments in descending order: 2, 3, 1, 4; segment I well developed ventrally; segment II narrower at base and thereafter widening, without clear denticle at posterior margin dorsally; segment III subrectangular with broadly rounded apex; segments II and III with extensive whitish enameling on dorsal surfaces. Hypostome (Fig. 3C): club-shaped; dental formula 3/3. Legs (Fig. 1A): of medium length, moderately robust; with extensive whitish enameling mostly on dorsal and lateral aspects of leg segments. Coxae (Fig. 3D and E): coxa I with relatively long, triangular, closely spaced internal and external spurs, internal spur broadly triangular with narrowly rounded apex, external spur narrowly triangular with broadly to narrowly rounded apex, internal and external spurs nearly equal in length, both spurs of coxa I generally directed posteriorly; coxae II and III each with moderate triangular external and internal spurs, external spur with narrowly rounded or tapering apex, internal spur with broadly or narrowly rounded apex; coxa IV with moderate triangular external spur with tapering apex and with several moderate triangular internal spurs, each with tapering apex; coxa IV enlarged, ratio length to width 0.81–1.10 ( $0.99 \pm 0.05$ ;  $n = 111$ ); coxae inornate or, especially coxae I, with small spots of whitish enameling. Trochanter I (Figs. 1A and 3F) with moderate, broadly triangular dorsal spur with tapering apex. Genu and Tibia (Fig. 1A) with two rows of very short projections ventrally. Genu IV length 0.75–1.29 ( $1.04 \pm 0.12$ ;  $n = 101$ ), width 0.37–0.66 ( $0.51 \pm 0.07$ ;  $n = 101$ ), ratio length to width 1.85–2.25 ( $2.02 \pm 0.07$ ;  $n = 101$ ).

**Female.** (redescription) (Figs. 1B and 4). Idiosoma (Fig. 1B): broadly oval, widest just anterior to mid-length. Scutum (Fig. 1B): length 1.87–2.69 ( $2.37 \pm 0.21$ ;  $n = 35$ ), width 2.16–2.85 ( $2.51 \pm 0.19$ ;  $n = 35$ ), ratio length to width 0.85–1.01 ( $0.94 \pm 0.04$ ;



**Fig. 1.** *Dermacentor bellulus*, dorsally. (A) Male (Taiwan, Taitung, Pei-yuan, Shih-nan, USNMENT 00714604). (B) Female (Taiwan, Taitung, Tung-ho, Pei-yuan, USNMENT 00714066). Scale bar = 1 mm.



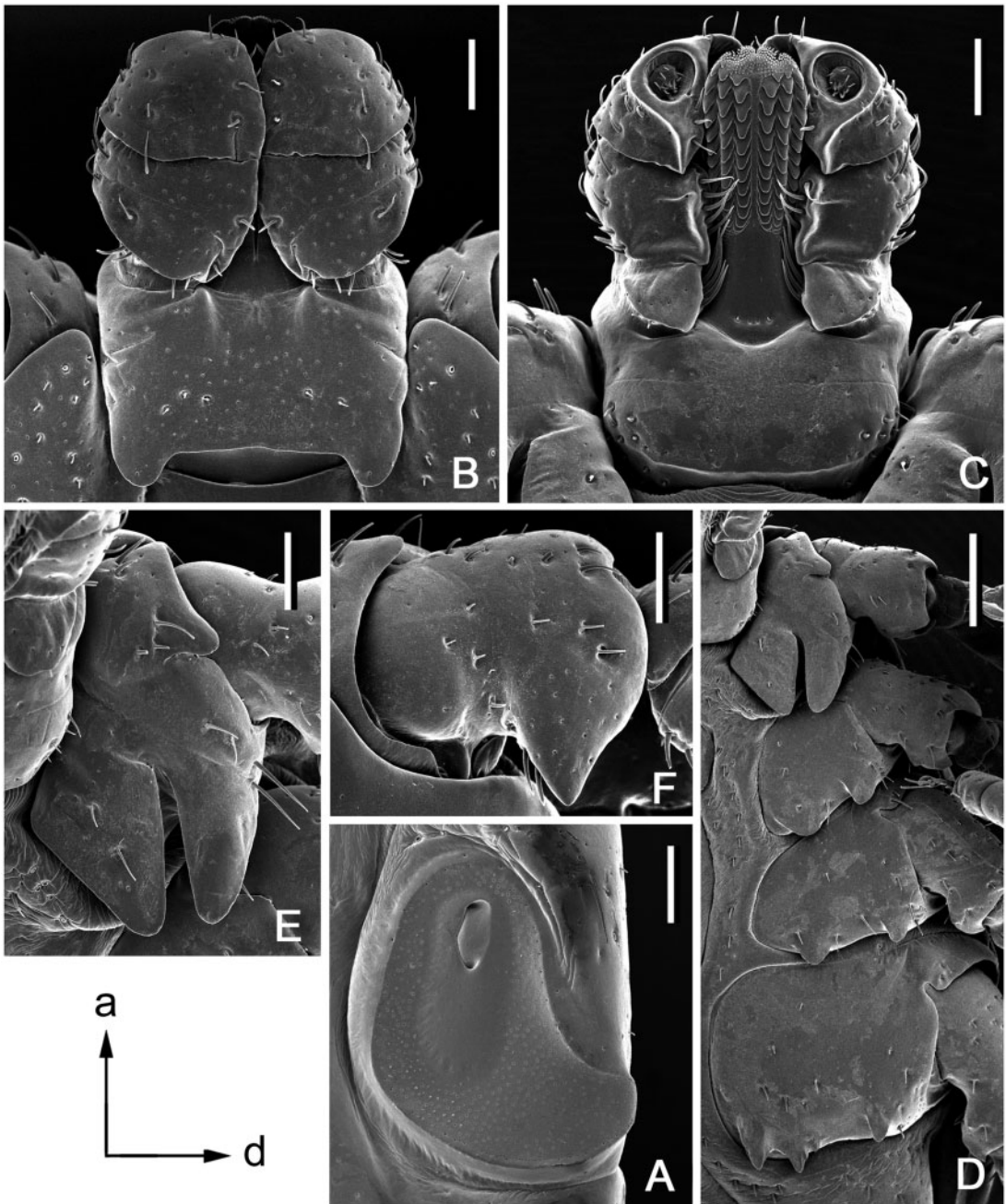
**Fig. 2.** (A–D) *Dermacentor bellulus*, variations in the coloration of male conscuta. (Taiwan, Taitung, Pei-yuan, Shih-nan, USNMNT 00714604). Scale bar = 1 mm.

$n = 35$ ), margins diverge posteriorly in anterior third of total length, thereafter gradually converging to broadly rounded posterior margin, posterolateral projections indistinct. Coloration: ornamentation very extensive, major portion of scutal surface covered with whitish enameling; brown colored patches arranged as follows: two pairs of small patches in cervical pits, a pair of narrow patches in cervical fields, large and broad central patch extending from anterior margin to posterior margin of scutum, hazy with speckles of small, darker patches, a pair of narrow patches bordering posterior margin of scutum extending from just anterior to eyes, widening at posterior margin of cervical grooves and connecting at posterior apex of scutum. Cervical grooves distinct, moderately deep. Surface of scutum smooth; very large and deep punctations moderately dense to fairly sparse and situated mostly in cervical grooves and anterior part of central field; fine punctations dense, evenly distributed over scutum. Eyes oval, very slightly convex, positioned at second third of scutal length. Setae relatively sparse and short. Alloscutum (Fig. 1B): as illustrated; 11 festoons. Setae of alloscutum relatively short (ca. 0.061), moderately dense. Genital aperture (Fig. 4A and B): at level of coxae II, moderately narrow and U-shaped, semi-oval sclerites bordering genital aperture laterally distinct; preatrial fold conspicuously bulging. Spiracular plates (Fig. 4C): suboval; dorsal prolongation moderately long and broad, broadly rounded to its apex, with broad unperforated widening anteriorly; perforations very small and fairly numerous. Gnathosoma (Figs. 1B, 4D and E): length from palpal apices to posterior margin of basis capituli dorsally 1.12–1.52 ( $1.34 \pm 0.10$ ;  $n = 34$ ), width of basis capituli 0.86–1.17 ( $1.03 \pm 0.08$ ;  $n = 34$ ), ratio length to width 1.18–1.40 ( $1.30 \pm 0.05$ ;  $n = 34$ ). Basis capituli (Figs. 1B, 4D and E): dorsally subrectangular; posterior margin nearly straight or slightly concave, length 0.42–0.59 ( $0.50 \pm 0.04$ ;  $n = 34$ ), ratio width to length 1.79–2.32 ( $2.08 \pm 0.11$ ;  $n = 34$ ); cornua broad, short, total length of basis capituli, including cornua, 5.90–11.00 ( $8.53 \pm 1.32$ ;  $n = 34$ ) cornual length; dorsally extensively ornate with whitish enameling. Porose areas moderate, circular, deeply sunken with clearly

circumscribed borders, separated by space less than their width. Basis capituli ventrally subrectangular, with convex posterior margin. Palpi (Figs. 1B, 4D and E): short and broad; length dorsally (segments I–III) 0.70–0.96 ( $0.85 \pm 0.06$ ;  $n = 35$ ), width 0.36–0.54 ( $0.46 \pm 0.05$ ;  $n = 35$ ), ratio length to width 1.67–2.10 ( $1.86 \pm 0.10$ ;  $n = 35$ ), length of segments in descending order: 2, 3, 1, 4; segment I well developed ventrally; segment II narrower at base and thereafter parallel-sided, without clear denticle at posterior margin dorsally; segment III broad, subrectangular with broadly rounded apex; segments II and III with extensive whitish enameling on dorsal surfaces. Hypostome (Fig. 4E): club-shaped; dental formula 3/3. Legs (Fig. 1B): of medium length, slender; extensively ornate with whitish enameling mostly on dorsal and lateral aspects of leg segments. Coxae (Fig. 4F and G): coxa I with relatively long, triangular, closely spaced internal and external spurs, internal spur broadly triangular with narrowly rounded apex, external spur narrowly triangular with broadly to narrowly rounded apex, internal and external spurs nearly equal in length, both spurs of coxa I generally directed posteriorly; coxae II and III each with moderate triangular external and internal spurs, external spur with narrowly rounded or tapering apex, internal spur with broadly rounded apex on coxa II and narrowly to broadly rounded apex on coxa III; coxa IV with moderate triangular subequal external and internal spurs, each with narrowly rounded to tapering apex; coxae inornate or, especially coxae I, with small spots of ivory enameling. Trochanter I (Figs. 1B and 4H) with moderate, broadly triangular dorsal spur with tapering apex. Genu IV length 0.81–1.16 ( $1.02 \pm 0.08$ ;  $n = 33$ ), width 0.37–0.56 ( $0.46 \pm 0.05$ ;  $n = 33$ ), ratio length to width 2.06–2.43 ( $2.22 \pm 0.08$ ;  $n = 33$ ).

**Nymph.** (redescription) (Fig. 5). Idiosoma: suboval, widest at level of posterior margin of coxae IV. Scutum (Fig. 5A): length 670–730 ( $703 \pm 25$ ;  $n = 5$ ), width 610–690 ( $659 \pm 30$ ;  $n = 5$ ), ratio length to width 1.06–1.10 ( $1.07 \pm 0.02$ ;  $n = 5$ ); pentagonal, anterolateral margins slightly diverging, subparallel; posterolateral margins converging to moderately narrow rounded apex, posterolateral depressions and posterolateral

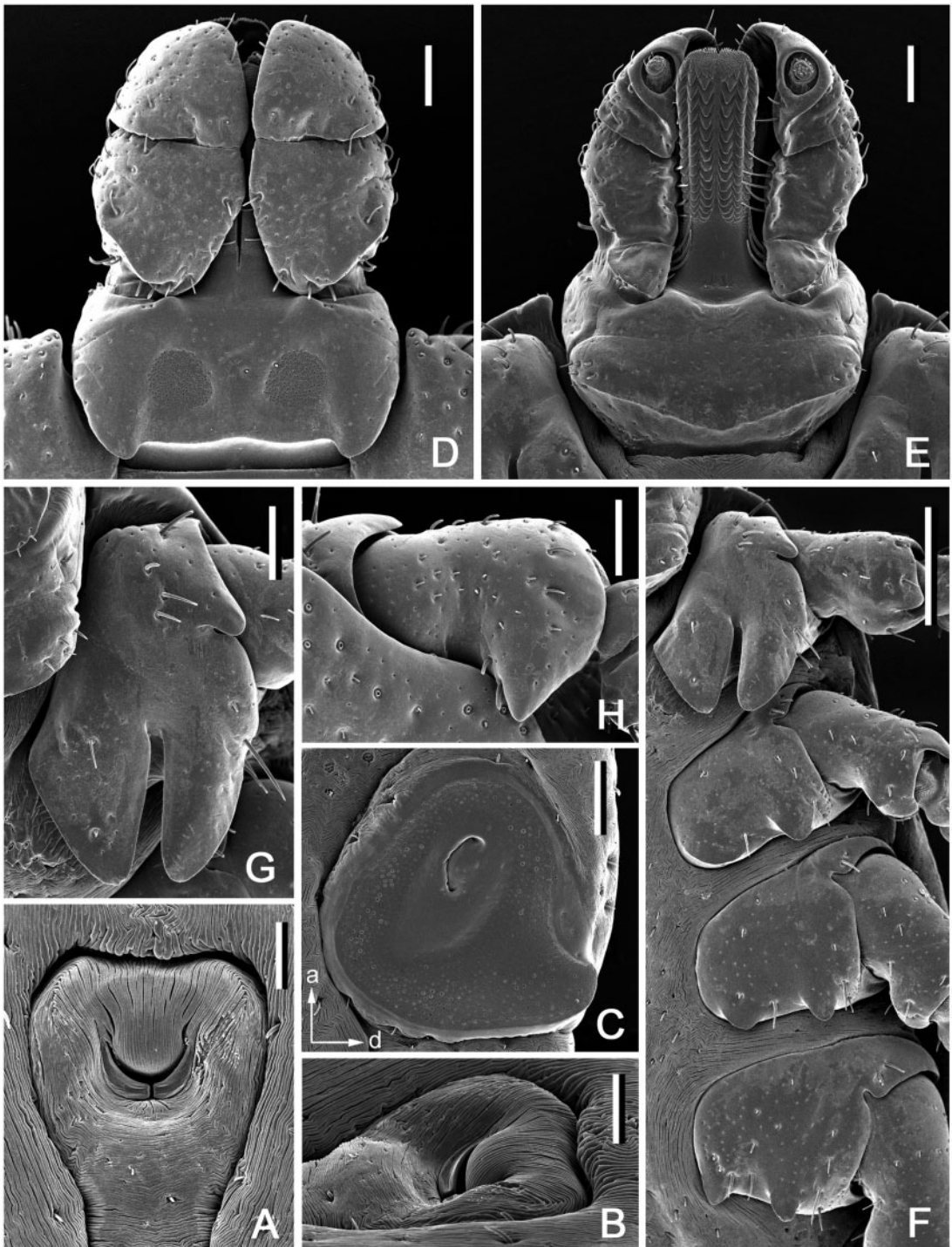




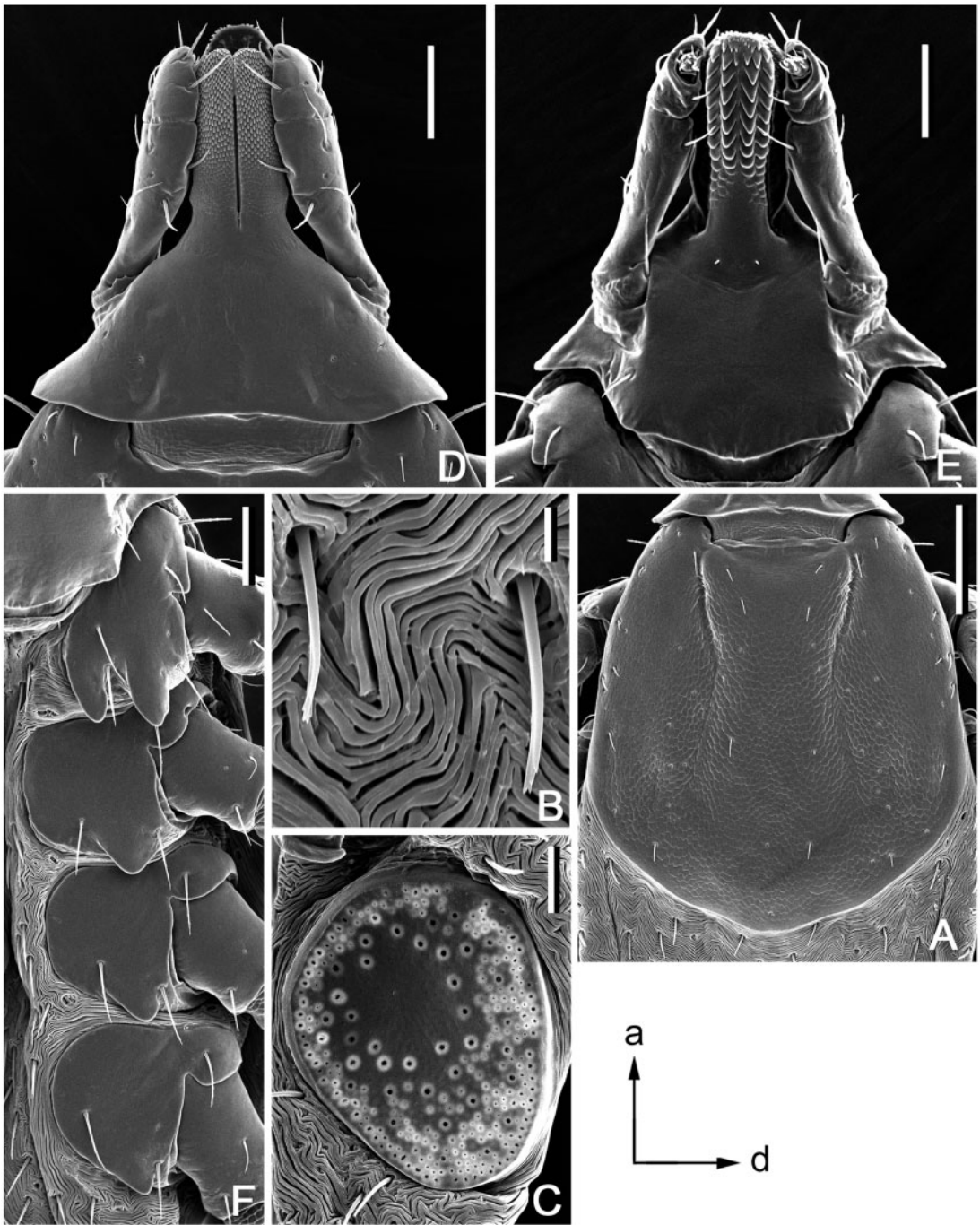
**Fig. 3.** *Dermacentor bellulus*, male (Taiwan, Taitung, Tung-ho, Pei-yuan, USNMNT 00714291). (A) Spiracular plate. Scale bar = 0.2 mm. Arrows show orientation of spiracular plate (a—anterior; d—dorsal). (B) Gnathosoma dorsally. Scale bar = 0.2 mm. (C) Gnathosoma ventrally. Scale bar = 0.2 mm. (D) Coxae. Scale bar = 0.5 mm. (E) Coxa I. Scale bar = 0.2 mm. (F) Trochanter I. Scale bar = 0.2 mm.

angles slight; cervical grooves distinct, shallow. Setae approximately 12–18 (14;  $n = 5$ ) pairs, length of setae in posterior portion of central field 30–36 ( $33 \pm 2$ ;  $n = 5$ ). Eyes suboval, slightly bulging, located on lateral margins of scutum at posterior third of its length; length of scutum portion posterior to eyes 210–230 ( $220 \pm 7$ ;  $n = 5$ ), ratio of scutum length to length of its

portion posterior to eyes 3.04–3.48 ( $3.22 \pm 0.18$ ;  $n = 5$ ). Number of pairs of dorsal setae on alloscutum 47–54 (50;  $n = 4$ ); length of setae in anterolateral portion of alloscutum 47–54 ( $51 \pm 3$ ;  $n = 5$ ); setae in central rows length 39–46 ( $41 \pm 3$ ;  $n = 5$ ); setae with denticles (Fig. 5B). Fovea with two or three (in one case, four) openings. Two to four pairs of setae at the level of



**Fig. 4.** *Dermacentor bellulus*, female (Taiwan, Taitung, Tung-ho, Pei-yuan, USNM 00714291). (A) Genital aperture, ventral view. Scale bar = 0.1 mm. (B) Genital aperture, ventrolateral view. Scale bar = 0.1 mm. (C) Spiracular plate. Scale bar = 0.2 mm. Arrows show orientation of spiracular plate (a—anterior; d—dorsal). (D) Gnathosoma dorsally. Scale bar = 0.2 mm. (E) Gnathosoma ventrally. Scale bar = 0.2 mm. (F) Coxae. Scale bar = 0.5 mm. (G) Coxa I. Scale bar = 0.2 mm. (H) Trochanter I. Scale bar = 0.2 mm.



**Fig. 5.** *Dermacentor bellulus*, nymph (Taiwan, Taipei, Ta-t'un Shan, Pai-liu-chia, USNMENT 00714074). (A) Scutum. Scale bar = 200  $\mu$ m. (B) Setae of alloscutum. Scale bar = 10  $\mu$ m. (C) Spiracular plate. Scale bar = 50  $\mu$ m. Arrows show orientation of spiracular plate (a—anterior; d—dorsal). (D) Gnathosoma dorsally. Scale bar = 100  $\mu$ m. (E) Gnathosoma ventrally. Scale bar = 100  $\mu$ m. (F) Coxae. Scale bar = 100  $\mu$ m.

coxae II ventrally. Spiracular plates (Fig. 5C): irregularly oval, moderate to large, greatest diameter in antero-posterior plane, longitudinal diameter of spiracular plate considerably larger than longitudinal

diameter of sclerite around anal valves; submarginal row of perforations complete. Gnathosoma (Fig. 5D and E): length from palpal apices to posterior dorsal margin of basis capituli 340–395 ( $368 \pm 23$ ;  $n = 5$ ),

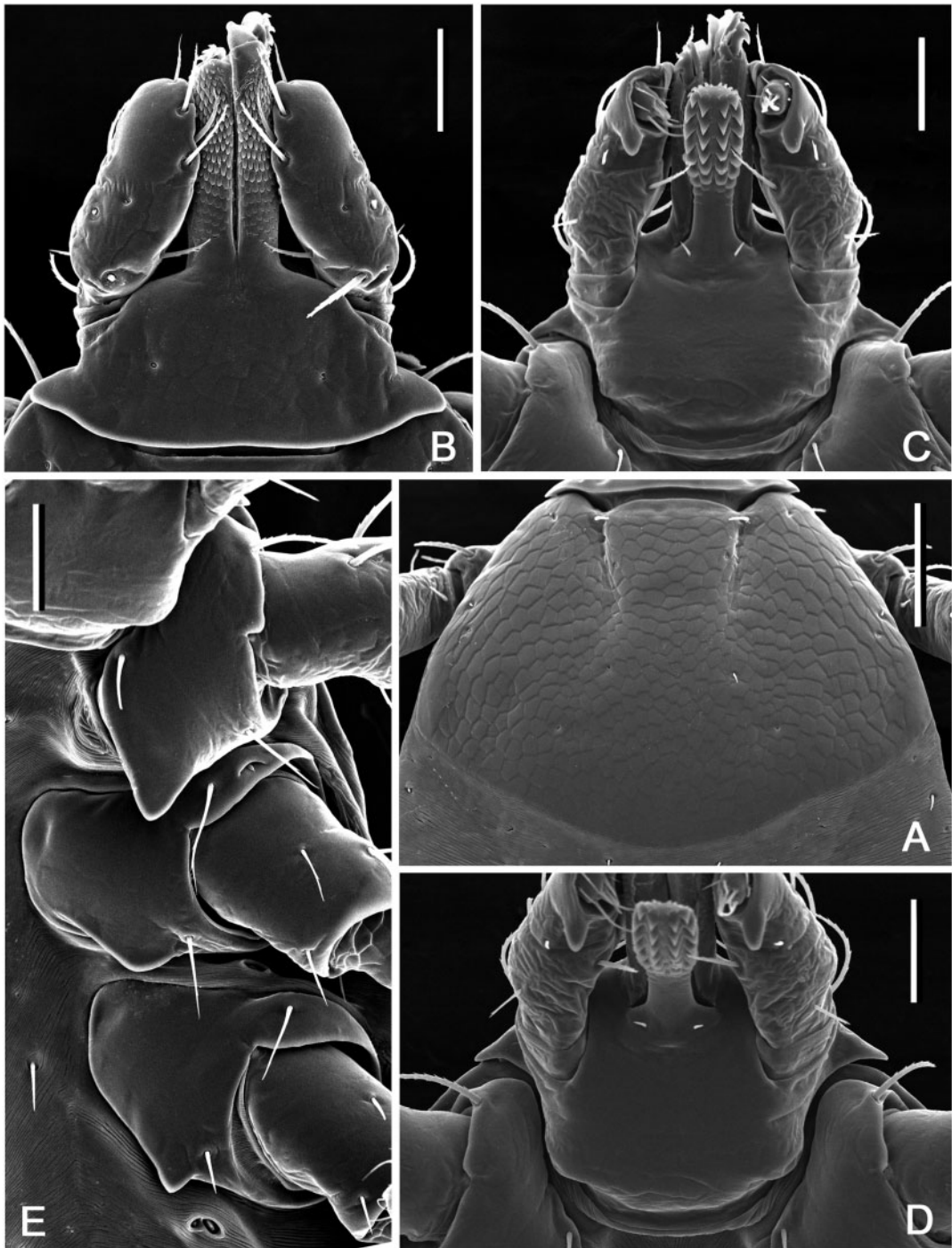
width at apices of dorsolateral projections 402–460 ( $438 \pm 24$ ;  $n=5$ ); ratio length to width 0.80–0.90 ( $0.84 \pm 0.04$ ;  $n=5$ ). Basis capituli (Fig. 5D and E): dorsally subtriangular, with very long and sharply pointed lateral projections; lacking auriculae ventrally; with two pairs of ventral setae and one pair of posthypostomal setae. Palpi (Fig. 5D and E): elongate, length (segments II–III) 252–292 ( $278 \pm 16$ ;  $n=5$ ), maximum width 60–67 ( $64 \pm 3$ ,  $n=5$ ), ratio length to width 4.18–4.55 ( $4.33 \pm 0.14$ ;  $n=5$ ); segment I well developed ventrally, cylindrical, clear suture between segments II and III, segment II the longest, narrow proximally and gradually expanding distally, segment III broadly rounded at apex; segment I with one ventral seta, segment II with four dorsal and three ventral setae, segment III with five dorsal and two ventral setae. Hypostome (Fig. 5E): length from apex to level of posthypostomal setae 202–232 ( $220 \pm 12$ ;  $n=5$ ), width at narrowest portion 60–77 ( $68 \pm 7$ ;  $n=2$ ), ratio length to width 3.00–3.44 ( $3.26 \pm 0.19$ ;  $n=5$ ); club-shaped; dental formula: distal 1 row on either side (rarely on both sides) of larger denticles 3/3, proximal approximately 7–8 rows 2/2; 3/3 portion of hypostome comprises approximately 1/10 of its total length (ratio avg. 10.08). Coxae (Fig. 5F): coxa I with relatively long internal and external spurs; internal spur slightly shorter than external; both spurs triangular with bluntly tapering apices; external spur on coxae II–IV relatively large, broadly triangular with bluntly tapering apices; size of external spurs slightly decreasing from coxa II to coxa IV; coxa II without distinct internal spur; spur on coxa IV usually not protruding beyond posterior coxal margin; coxal “pores” (openings of dermal glands or sensilla usually situated close to mid-margin of coxae) present only on coxae I (rarely asymmetrically present on other coxae). Genu IV: length 255–285 ( $269 \pm 15$ ;  $n=5$ ), width 95–107 ( $102 \pm 7$ ;  $n=3$ ), ratio length to width 2.65–2.74 ( $2.70 \pm 0.04$ ;  $n=3$ ).

**Larva.** (Fig. 6). Idiosoma: suboval, widest at level of coxae III. Scutum (Fig. 6A): length 320–345 ( $332 \pm 7$ ;  $n=15$ ), width 435–480 ( $455 \pm 13$ ;  $n=15$ ), ratio length to width 0.71–0.77 ( $0.73 \pm 0.01$ ;  $n=15$ ); pentagonal, posterior margin broadly rounded, post-erolateral marginal depressions slight; cervical grooves as faint, shallow depressions. Eyes suboval, slightly bulging, located on lateral margins of scutum in posterior third of scutum length; length of scutum portion posterior to eyes 95–115 ( $106 \pm 6$ ;  $n=15$ ), ratio of scutum length to length of its portion posterior to eyes 2.95–3.42 ( $3.14 \pm 0.14$ ;  $n=15$ ). Setae 3 pairs,  $Sc_2$  19–22 ( $20 \pm 1$ ;  $n=5$ ),  $Sc_3$  16–19 ( $17 \pm 1$ ;  $n=5$ ). Dorsal setae of alloscutum 10 pairs; 2 pairs of central dorsals,  $Cd_1$  17–20 ( $19 \pm 1$ ;  $n=10$ ),  $Cd_2$  19–21 ( $20 \pm 1$ ;  $n=5$ ); 8 pairs of marginal dorsals,  $Md_1$  21–26 ( $23 \pm 2$ ;  $n=6$ ),  $Md_8$  17–21 ( $18 \pm 1$ ;  $n=10$ ). Ventral setae 14 pairs plus 1 pair on anal valves; 3 pairs of sternals,  $St_1$  35–40 ( $37 \pm 1$ ;  $n=11$ ); 2 pairs of preanals,  $Pa_1$  26–32 ( $29 \pm 2$ ;  $n=9$ ),  $Pa_2$  25–29 ( $27 \pm 2$ ;  $n=8$ ); 4 pairs of premarginals,  $Pm_1$  28–37 ( $31 \pm 2$ ;  $n=10$ ); 5 pairs of marginal ventrals,  $Mv_1$  18–24 ( $21 \pm 2$ ;  $n=13$ ),  $Mv_5$  17–21 ( $20 \pm 1$ ;  $n=14$ ).

Gnathosoma (Fig. 6B–D): length from palpal apices to posterior dorsal margin of basis capituli 167–195 ( $180 \pm 8$ ;  $n=15$ ), width at apices of dorsolateral projections 200–222 ( $213 \pm 7$ ;  $n=15$ ); ratio length to width 0.80–0.90 ( $0.84 \pm 0.03$ ;  $n=15$ ). Basis capituli (Fig. 6B–D): dorsally subtriangular, with long and tapering lateral projections; ventrally rectangular; anterior angle of basis capituli slightly obtuse; auriculae as short, broad, and blunt projections. Posthypostomal setae 1 pair. Palpi (Fig. 6B–D): elongate, length (segments II–III) 122–135 ( $130 \pm 4$ ;  $n=15$ ), width 50–55 ( $52 \pm 1$ ,  $n=15$ ), ratio length to width 2.38–2.65 ( $2.49 \pm 0.07$ ;  $n=15$ ); segment I well developed ventrally, cylindrical, faint suture between segments II and III, segment III with relatively large denticle ventrally; segment I without setae, segment II with four dorsal and two ventral setae, segment III with five dorsal and one ventral setae. Hypostome (Fig. 6C): length from apex to level of posthypostomal setae 92–105 ( $98 \pm 3$ ;  $n=14$ ), minimum width 26–30 ( $28 \pm 1$ ;  $n=14$ ), ratio length to width 3.36–3.64 ( $3.49 \pm 0.08$ ;  $n=14$ ); club-shaped, dental formula 2/2 throughout length, ca. 6 larger denticles in median files; denticulated portion comprises approximately half of hypostomal length. Coxae (Fig. 6E): coxa I with large triangular spur with tapering apex, coxae II and III each with relatively large triangular spurs. Genu I: length 150–170 ( $161 \pm 6$ ;  $n=15$ ), width 67–77 ( $74 \pm 3$ ;  $n=13$ ), ratio length to width 2.03–2.28 ( $2.18 \pm 0.08$ ;  $n=13$ ).

**HOLOTYPE.** Male, from dog, Kosempo (23° 42' N, 121° 3' E), Nantou County, Taiwan, collected by Sauter. Schulze (1935) indicated that this specimen is in the Entomological Institute Berlin-Dahlem (Germany). All noninsect specimens from the Senckenberg Deutsches Entomologisches Institut (Senckenberg German Entomological Institute, Müncheberg) were transferred to the Museum für Naturkunde (Berlin) but unfortunately the type specimen of *D. bellulus* was not among them (Jason Dunlop, personal communication). We were unable to confirm the existence of the holotype. Based on the original description and illustrations, it is clear that Schulze (1935) had additional specimens of *D. bellulus* (paratypes) but their whereabouts are also unknown.

The male of *D. bellulus* was described and illustrated by Schulze (1935). Later, a male of this species was described and illustrated in Sugimoto (1937) as *D. atrosignatus*. Keegan and Toshioka (1957) referred to this taxon as *Dermacentor* sp., as did Yamaguti et al. (1971). Wassef and Hoogstraal (1986a) illustrated the male as *D. taiwanensis* but provided a description that was based on specimens of both *D. taiwanensis* and *D. bellulus*. Apparently, the first and only description of the female of *D. bellulus* is that of Sugimoto (1937), again as *D. atrosignatus*. Unfortunately, however, key features are not illustrated and it is therefore difficult to ascertain the identity of Sugimoto's female specimen. The nymph and larva of *D. bellulus* were described by Kitaoka and Suzuki (1981) as *D. taiwanensis* and later reproduced in Teng and Jiang (1991), also as *D. taiwanensis*.



**Fig. 6.** *Dermacentor bellulus*, larva (Taiwan, Taipei, San-chih, Ch'e-Ch'eng, USNM 00714185). (A) Scutum. Scale bar = 100  $\mu$ m. (B) Gnathosoma dorsally. Scale bar = 50  $\mu$ m. (C) Gnathosoma ventrally. Scale bar = 50  $\mu$ m. (D) Gnathosoma anteroventrally. Scale bar = 50  $\mu$ m. (E) Coxae. Scale bar = 50  $\mu$ m.

**Synonyms.** *Indocentor bellulus* Schulze, 1935.

Schulze (1935) originally described *D. bellulus* in the genus *Indocentor*. Luh and Woo (1950) moved this species to the genus *Dermacentor*.

**Hosts.** The host data for *D. bellulus* are summarized in Table 1. Most adults have been collected from wild boar, *Sus scrofa* L. A few adults are from giant panda, *Ailuropoda melanoleuca* (David), Asian black bear,

*Ursus thibetanus* Cuvier, and unidentified bear, *Ursus* sp. A single male was taken from a human and a single female was collected off clothing. The type specimens were collected from domestic dog (Schulze, 1935). Both nymphs and larvae were collected from Chinese hare, *Lepus sinensis* Gray, greater bandicoot rat, *Bandicota indica* (Bechstein), Losea rat, *Rattus losea* (Swinhoe), brown rat, *Rattus norvegicus* (Berkenhout), roof rat, *Rattus rattus* (L.), rats, *Rattus* sp., and unidentified "rats." Additionally, nymphs have been found on large Japanese field mouse, *Apodemus speciosus* (Temminck), Confucian niviventer, *Niviventer confucianus* (Milne-Edwards), spiny Taiwan niviventer, *Niviventer coninga* (Swinhoe), niviventer, *Niviventer* sp., Oriental house rat, *Rattus tanezumi* Temminck, common tree-shrew, *Tupaia glis* (Diard) and clothing, while larvae have been recorded from lesser bandicoot rat, *Bandicota bengalensis* (Gray), Ryukyu mouse, *Mus caroli* Bonhote, unidentified "rodents," Chinese ferret-badger, *Melogale moschata* (Gray), and Chinese bamboo-partridge *Bambusicola thoracicus* (Temminck).

Adults apparently can be collected throughout the year. In material that we have studied, adult *D. bellulus* were collected during all months except July and September, with the maximum number of collections made in February. Nymphs of *D. bellulus* were collected during all months except February, with the maximum number of collections made in April, while larvae were collected during all months except January, with the maximum number of collections in March.

**Distribution.** (Fig. 7). Distribution data for *D. bellulus* are summarized in Table 1. The known distribution of this species is confined to China (Fujian, Sichuan, and Tibet Provinces), Japan (Fukui, Kagoshima, Kanagawa, and Kyoto Prefectures), Nepal (Nuwakot and Rasuwa Districts), Taiwan (Taipei and Taitung Counties), and Vietnam (Da Nang, Dak Lak, Dong Nai, Lam Dong, Lao Cai, Quang Binh, and Quang Tri Provinces). This is the only *Indocentor* species occurring in both the Oriental and Palearctic Zoogeographic Regions.

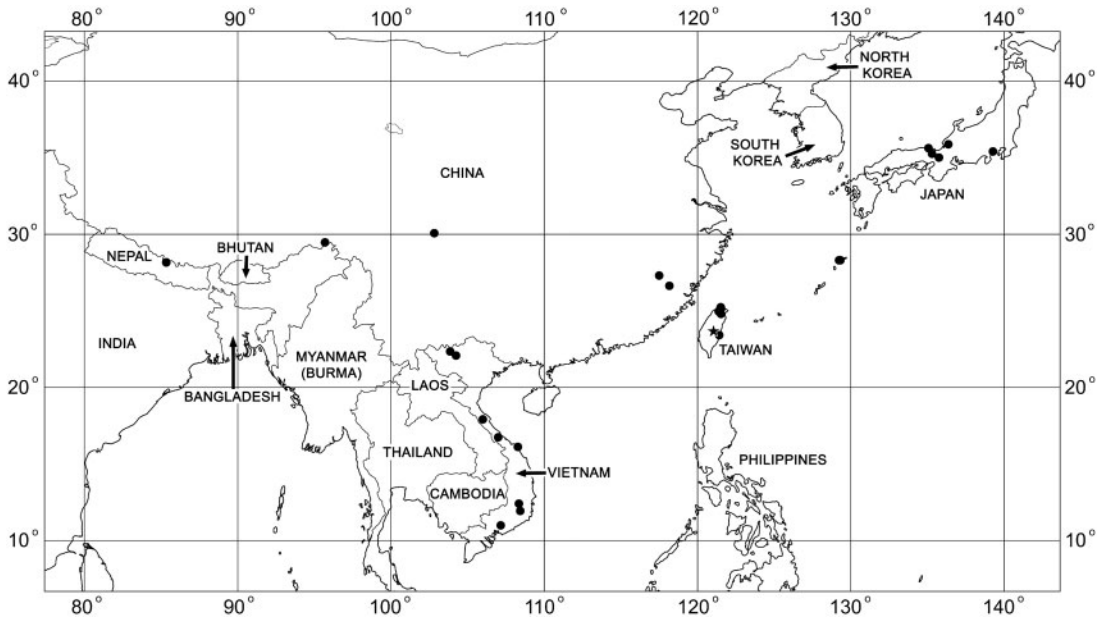
**Etymology.** The specific name is derived from the Latin "*bellulus*," meaning "beautiful," and apparently refers to the extensive bright ivory ornamentation of the male conscutum.

#### *Dermacentor taiwanensis* Sugimoto, 1935

(Figs. 8–12)

**Male.** (redescription) (Figs. 8A and 9). Conscutum (Fig. 8A): broadly oval with distinctly convex lateral margins, widest approximately at mid-length; distance from scapular apices to posterior margin of conscutum 2.87–5.94 ( $4.99 \pm 0.68$ ;  $n = 55$ ), maximum width 2.31–4.81 ( $3.89 \pm 0.54$ ;  $n = 55$ ), ratio length to width 1.22–1.37 ( $1.28 \pm 0.03$ ;  $n = 55$ ). Coloration as illustrated: pale ivory-colored ornamentation very extensive, light- to dark-brown background forms several patches, often with indistinct hazy margins; a pair of narrow cervical patches extending from cervical pits to posterior margin of pseudoscutum; a pair of small patches lateral to cervical patches; broad, well-defined anterior and

hazy posterior brownish central patch on pseudoscutum; posteromedian margin of pseudoscutum indicated by narrow hazy strip; lateral field with one narrow brown patch extending along most of lateral margins of conscutum from eyes to first festoon; two pairs of oval patches medial to lateral grooves; a pair of central patches; narrow stripes on posteromedian and paramedian regions; first, second, and paramedian festoons mostly ivory colored, third and fourth festoons mostly brown, median festoon with large ivory spot; all punctations light- to dark-brown. Central field posterior to pseudoscutum often is flat, imparting a concave appearance to conscutum; surface of conscutum smooth. Cervical grooves shallow; a pair of central depressions, and a second posterior pair that correspond to paramedian grooves; lateral grooves superficial, but distinct because they align with large punctations; 11 distinct festoons, median festoon conspicuously narrower than paramedian. Very large and deep punctations moderately dense, distributed over entire conscutum but denser laterally and posteriorly; large punctations on pseudoscutum fairly sparse; fine punctations dense, evenly distributed. Eyes oval, very slightly convex, at anterior one-fifth of conscutal length. Setae relatively short and inconspicuous. Spiracular plates (Fig. 9A): suboval; dorsal prolongation moderately long and broad, with broad, unperforated widening anteriorly; perforations very small and fairly numerous. Sclerotized plaques on festoons ventrally inornate or with small ivory-colored spot. Gnathosoma (Figs. 8A, 9B and C): length from palpal apices to cornual apices dorsally 0.70–1.41 ( $1.21 \pm 0.14$ ;  $n = 54$ ), width of basis capituli 0.49–1.00 ( $0.85 \pm 0.10$ ;  $n = 54$ ), ratio length to width 1.27–1.53 ( $1.42 \pm 0.05$ ;  $n = 54$ ). Basis capituli (Figs. 8A, 9B and C): dorsally subrectangular; posterior margin nearly straight or slightly concave; length 0.30–0.60 ( $0.52 \pm 0.06$ ;  $n = 54$ ), ratio width to length 1.51–1.84 ( $1.65 \pm 0.07$ ;  $n = 54$ ); cornua broad, short, total length of basis capituli, including cornua, 4.67–9.33 ( $6.62 \pm 1.00$ ;  $n = 54$ ) cornual length; dorsally with extensive whitish enameling. Basis capituli ventrally subrectangular; posterior margin convex. Palpi (Figs. 8A, 9B and C): short, broad; length dorsally (segments I–III) 0.41–0.83 ( $0.70 \pm 0.08$ ;  $n = 54$ ), width 0.22–0.48 ( $0.39 \pm 0.05$ ;  $n = 54$ ), ratio length to width 1.58–2.16 ( $1.80 \pm 0.12$ ;  $n = 54$ ), length of segments in descending order: 2, 3, 1, 4; segment I well developed ventrally; segment II narrower at base and thereafter widening, without clear denticle at posterior margin dorsally; segment III subrectangular with broadly rounded apex; segments II and III with extensive whitish enameling on dorsal surfaces. Hypostome (Fig. 9C): club-shaped; dental formula 3/3. Legs (Fig. 8A): of medium length, moderately robust; with extensive whitish enameling mostly on dorsal and lateral aspects of leg segments. Coxae (Fig. 9D and E): coxa I with relatively long, triangular, closely spaced internal and external spurs, internal spur broadly triangular with narrowly rounded apex, external spur narrowly triangular with broadly to narrowly rounded apex, internal and external spurs nearly equal in length, both spurs of coxa I generally directed posteriorly; coxae II and III each with

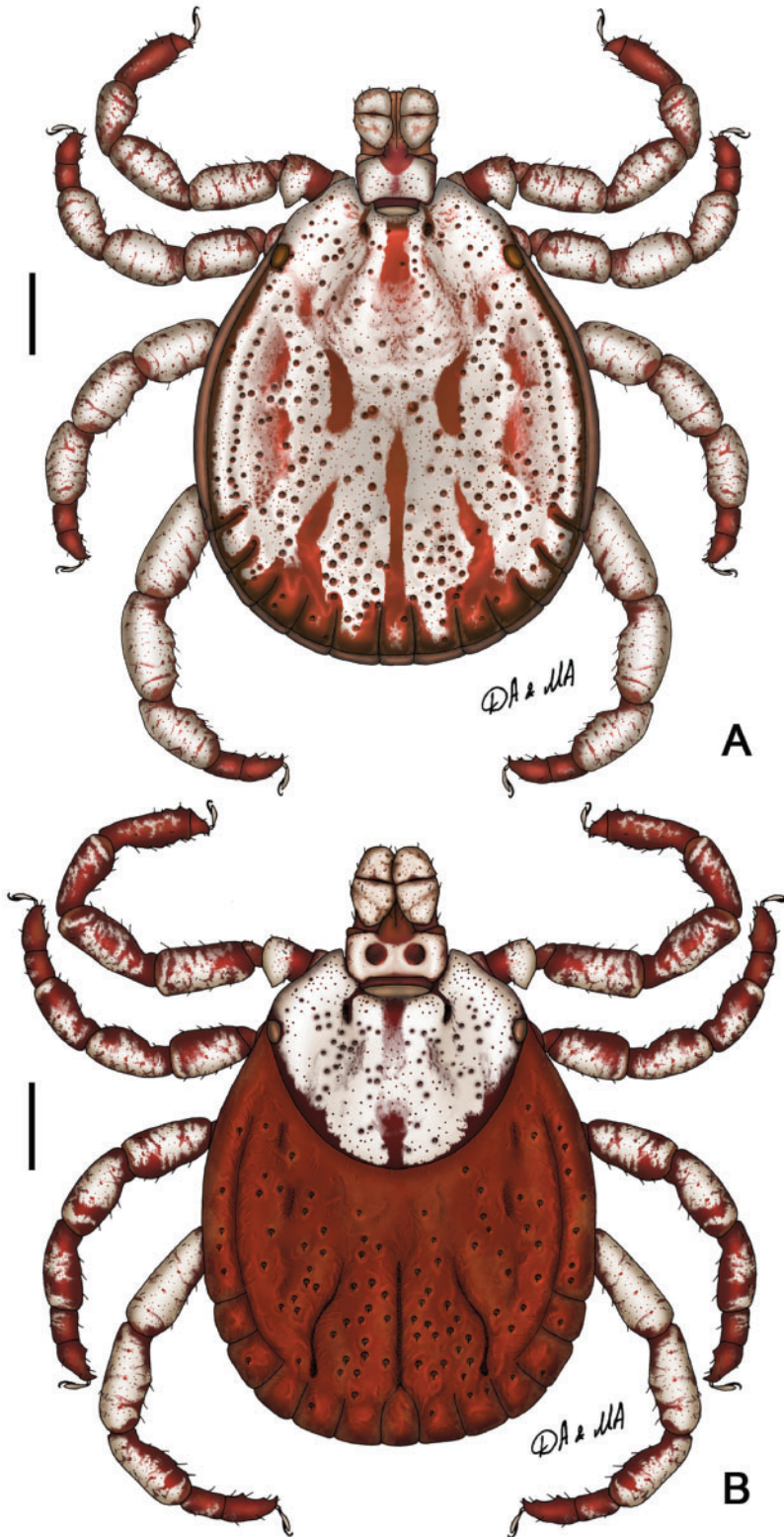


**Fig. 7.** *Dermacentor bellulus*, map of geographical distribution. Star shows type locality, filled circles show confirmed localities.

moderate triangular external and internal spurs, external spur with narrowly rounded or tapering apex, internal spur with broadly or narrowly rounded apex; coxa IV with moderate triangular external spur with tapering apex and with several moderate triangular internal spurs, each with tapering apex; coxa IV enlarged, ratio length to width 0.78–1.08 ( $0.95 \pm 0.08$ ;  $n = 55$ ). Trochanter I (Figs. 8A and 9F) with moderately long, broadly triangular dorsal spur with tapering apex. Genu and Tibia (Fig. 8A) with two rows of very short projections ventrally. Genu IV length 0.57–1.38 ( $1.12 \pm 0.17$ ;  $n = 53$ ), width 0.25–0.70 ( $0.53 \pm 0.10$ ;  $n = 53$ ), ratio length to width 1.86–2.35 ( $2.13 \pm 0.12$ ;  $n = 53$ ).

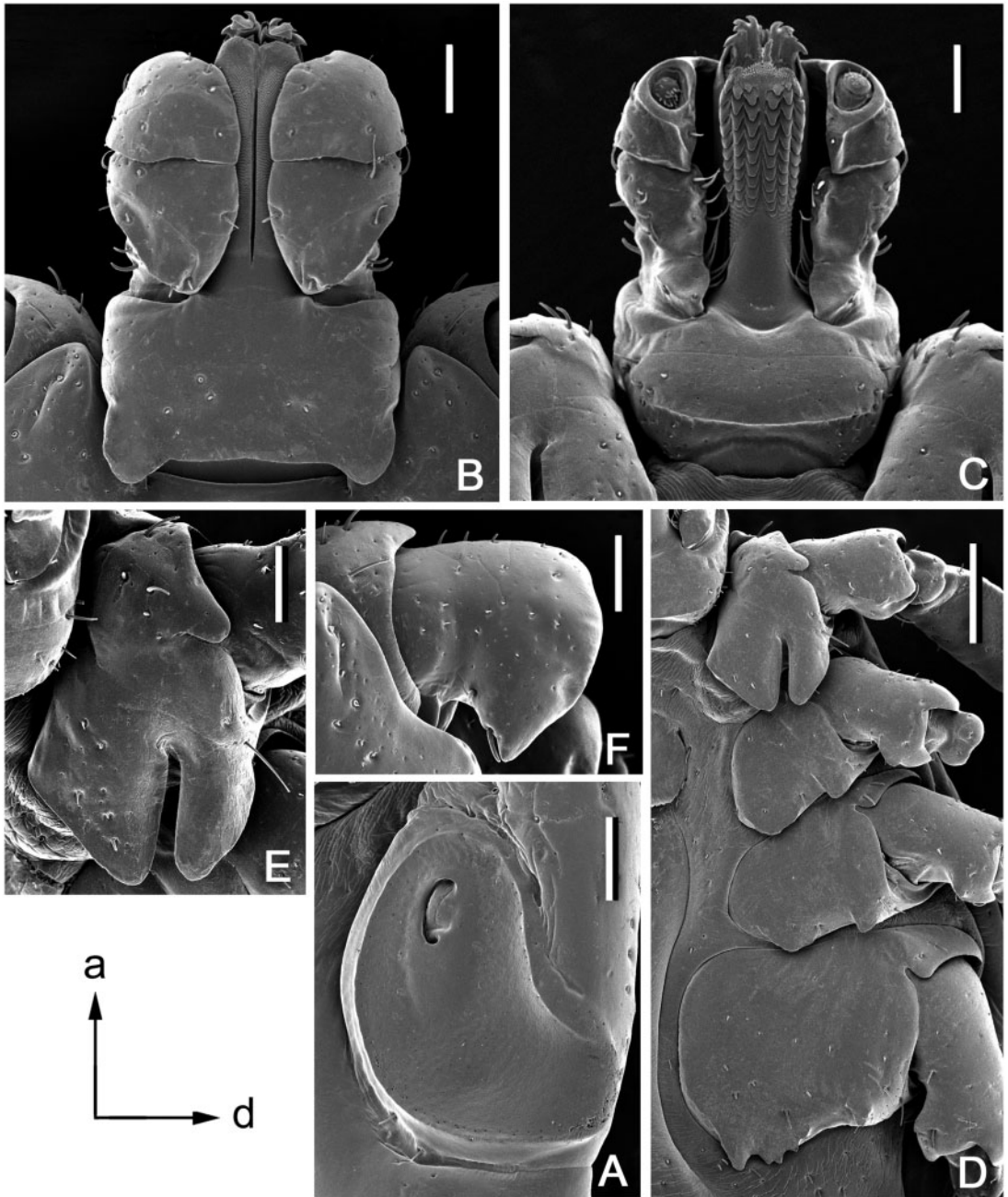
**Female.** (redescription) (Figs. 8B and 10). Idiosoma (Fig. 8B): broadly oval, widest near mid-length. Scutum (Fig. 8B): length 1.95–2.75 ( $2.41 \pm 0.19$ ;  $n = 23$ ), width 2.30–3.25 ( $2.88 \pm 0.23$ ;  $n = 23$ ), ratio length to width 0.76–0.90 ( $0.84 \pm 0.03$ ;  $n = 23$ ), margins diverge posteriorly in anterior third of total length, thereafter gradually converging to broadly rounded posterior margin, slight posterolateral angular projections may be present. Coloration: ornamentation very extensive, major portion of scutal surface covered with whitish enameling; brown colored patches arranged as follows: two pairs of small patches in cervical pits, a pair of narrow patches in cervical fields, narrow central patch brown anteriorly and posteriorly, hazy toward center and disappearing at center of scutum, a pair of narrow patches bordering posterior margin of scutum extending from just anterior to eyes, widening at posterior margin of cervical grooves, and connecting at posterior apex of scutum. Cervical grooves distinct, moderately deep. Surface of scutum smooth; very large

and deep punctations sparse and situated mostly in cervical grooves and anterior part of central field; fine punctations dense, evenly distributed over scutum. Eyes oval, very slightly convex, positioned at second third of scutal length. Setae relatively sparse and short. Alloscutum (Fig. 8B): as illustrated; 11 festoons. Setae of alloscutum relatively short (ca. 0.076), moderately dense. Genital aperture (Fig. 10A and B): at level of coxae II, broadly V-shaped, sclerites bordering genital aperture laterally small and indistinct; preatrial fold slightly convex. Spiracular plates (Fig. 10C): suboval; dorsal prolongation moderately long and broad, broadly rounded to its apex, with broad unperforated widening anteriorly; perforations very small and fairly numerous. Gnathosoma (Figs. 8B, 10D and E): length from palpal apices to posterior margin of basis capituli dorsally 1.22–1.58 ( $1.43 \pm 0.09$ ;  $n = 23$ ), width of basis capituli 0.90–1.20 ( $1.05 \pm 0.07$ ;  $n = 23$ ), ratio length to width 1.28–1.45 ( $1.36 \pm 0.05$ ;  $n = 23$ ). Basis capituli (Figs. 8B, 10D and E): dorsally subrectangular; posterior margin nearly straight or slightly concave, length 0.46–0.62 ( $0.54 \pm 0.04$ ;  $n = 23$ ), ratio width to length 1.79–2.35 ( $1.93 \pm 0.12$ ;  $n = 23$ ); cornua broad, short, total length of basis capituli, including cornua, 7.00–14.50 ( $9.07 \pm 1.52$ ;  $n = 23$ ) cornual length; dorsally extensively ornate with whitish enameling. Porose areas moderate, circular, deeply sunken with clearly circumscribed borders, separated by space nearly equal to their width. Basis capituli ventrally subrectangular; with convex posterior margin. Palpi (Figs. 8B, 10D and E): short and broad; length dorsally (segments I–III) 0.77–0.96 ( $0.88 \pm 0.05$ ;  $n = 23$ ), width 0.35–0.50 ( $0.44 \pm 0.04$ ;  $n = 23$ ), ratio length to width 1.82–2.25 ( $2.02 \pm 0.13$ ;  $n = 23$ ), length of segments in descending



**Fig. 8.** *Dermacentor taiwanensis*, dorsally. (A) Male (Taiwan, Taitung, Pei-yuan, USNMENT 00714776). (B) Female (Taiwan, Taitung, Pei-yuan, Shih-nan, USNMENT 00714182). Scale bar = 1 mm.

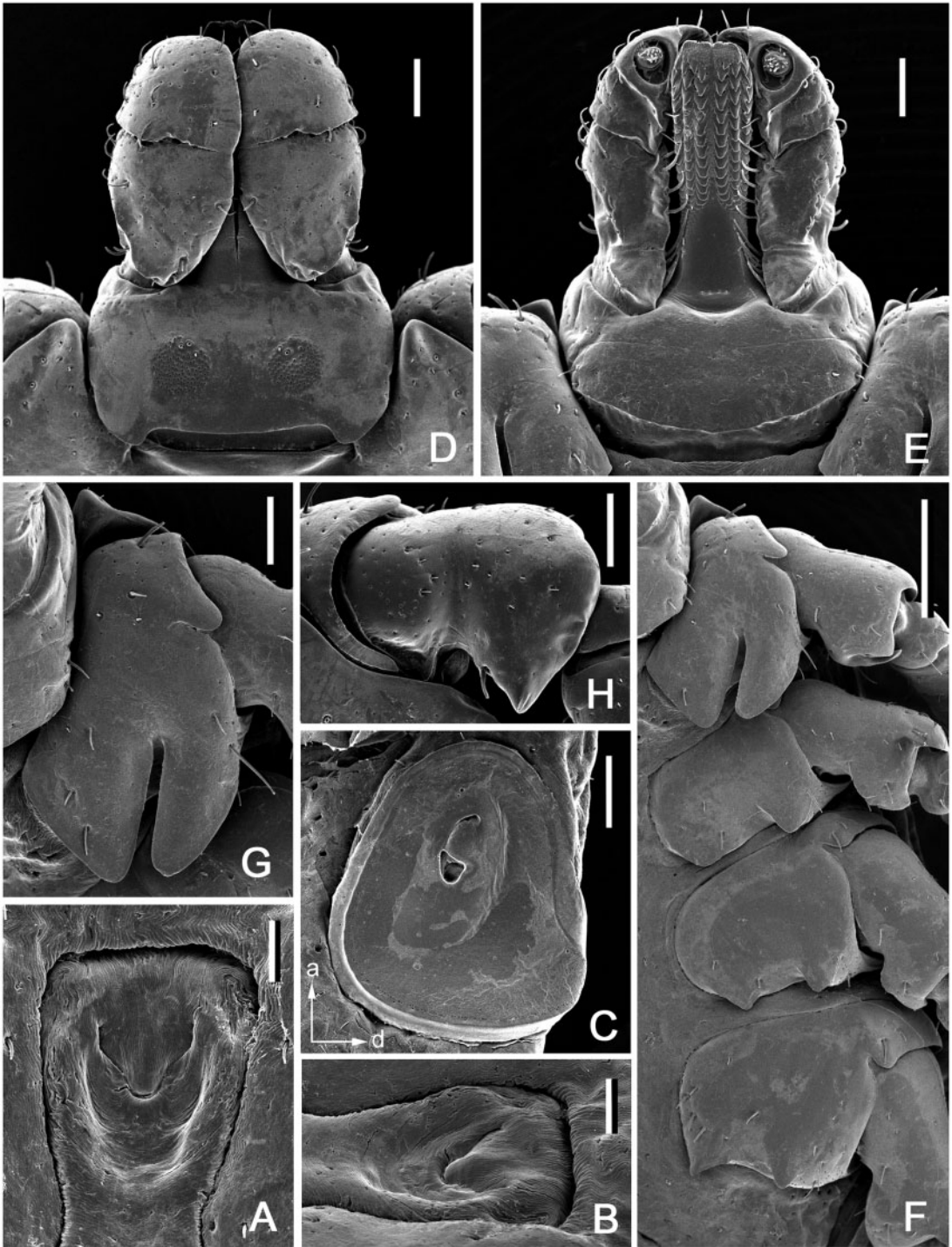




**Fig. 9.** *Dermacentor taiwanensis*, male (Taiwan, Taitung, Pei-yuan, USNMNT 00714776). (A) Spiracular plate. Scale bar = 0.2 mm. Arrows show orientation of spiracular plate (a—anterior; d—dorsal). (B) Gnathosoma dorsally. Scale bar = 0.2 mm. (C) Gnathosoma ventrally. Scale bar = 0.2 mm. (D) Coxae. Scale bar = 0.5 mm. (E) Coxa I. Scale bar = 0.2 mm. (F) Trochanter I. Scale bar = 0.2 mm.

order: 2, 3, 1, 4; segment I well developed ventrally; segment II narrower at base and thereafter parallel-sided, without clear denticle at posterior margin dorsally; segment III broad, subrectangular with broadly rounded apex; segments II and III with extensive whitish enameling on dorsal surfaces. Hypostome (Fig. 10E): club-shaped; dental formula 3/3. Legs (Fig. 8B):

of medium length, slender; extensively ornate with whitish enameling mostly on dorsal and lateral aspects of leg segments. Coxae (Fig. 10F and G): coxa I with relatively long, triangular, closely spaced internal and external spurs, internal spur broadly triangular with narrowly rounded apex, external spur narrowly triangular with broadly to narrowly rounded apex, internal and



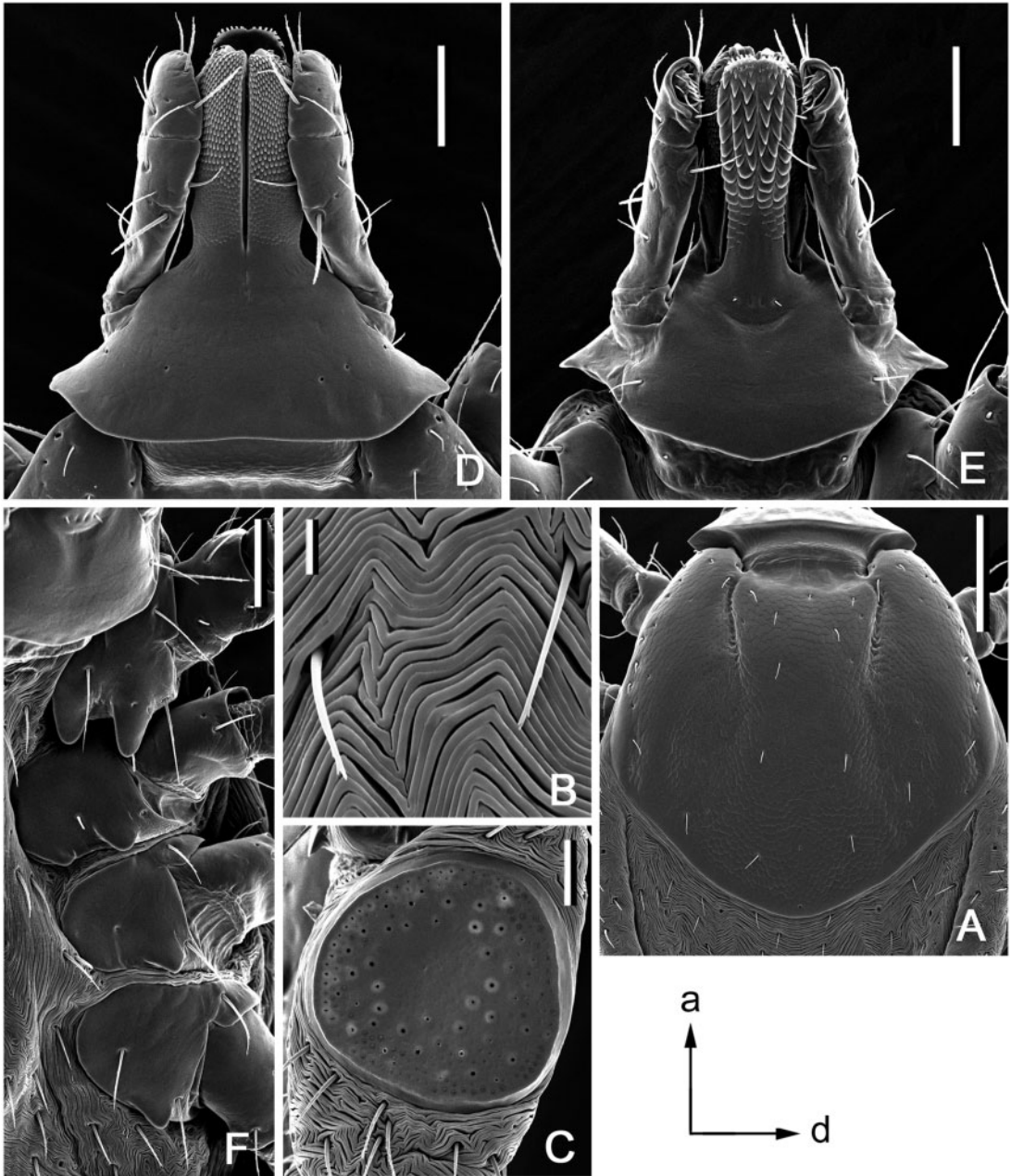
**Fig. 10.** *Dermacentor taiwanensis*, female (Taiwan, Taitung, Pei-yuan, Shih-nan, USNMENT 00714182). (A) Genital aperture, ventral view. Scale bar = 0.1 mm. (B) Genital aperture, ventrolateral view. Scale bar = 0.1 mm. (C) Spiracular plate. Scale bar = 0.2 mm. Arrows show orientation of spiracular plate (a—anterior; d—dorsal). (D) Gnathosoma dorsally. Scale bar = 0.2 mm. (E) Gnathosoma ventrally. Scale bar = 0.2 mm. (F) Coxae. Scale bar = 0.5 mm. (G) Coxa I. Scale bar = 0.2 mm. (H) Trochanter I. Scale bar = 0.2 mm.

external spurs nearly equal in length, both spurs of coxa I generally directed posteriorly; coxae II and III each with moderate triangular external and internal spurs, external spur with narrowly rounded or tapering apex, internal spur with broadly rounded apex on coxa II and narrowly to broadly rounded apex on coxa III; coxa IV with moderate triangular subequal external and internal spurs, with narrowly rounded to tapering apex; coxae inornate or, especially coxae I, with small spots of ivory enameling. Trochanter I (Figs. 8B and 10H) with moderate, broad, triangular dorsal spur with tapering apex. Genu IV length 0.96–1.30 ( $1.16 \pm 0.08$ ;  $n = 19$ ), width 0.42–0.57 ( $0.49 \pm 0.04$ ;  $n = 19$ ), ratio length to width 2.22–2.45 ( $2.34 \pm 0.07$ ;  $n = 19$ ).

**Nymph.** (description) (Fig. 11). Idiosoma: suboval, widest at level of posterior margin of coxae IV. Scutum (Fig. 11A): length 640–645 (642;  $n = 2$ ), width 650 ( $n = 2$ ), ratio length to width 0.98–0.99 (0.99;  $n = 2$ ); pentagonal, anterolateral margins distinctly diverging, posterolateral margins converging to moderately narrow rounded apex, posterolateral depressions and posterolateral angles very slight; cervical grooves distinct, shallow. Setae approximately 12–14 (13;  $n = 2$ ) pairs, length of setae in posterior portion of central field 29–32 (31;  $n = 2$ ). Eyes suboval, slightly bulging, located on lateral margins of scutum slightly posterior its midlength; length of scutum portion posterior to eyes 250–270 (260;  $n = 2$ ), ratio of scutum length to length of its portion posterior to eyes 2.39–2.56 (2.47;  $n = 2$ ). Number of pairs of dorsal setae on alloscutum 43–44 ( $n = 2$ ); length of setae in anterolateral portion of alloscutum 35–40 (37;  $n = 2$ ); setae in central rows length 31–32 (32;  $n = 2$ ); setae with denticles (Fig. 11B). Fovea with two or three (one to four) openings. Two pairs of setae at the level of coxae II ventrally. Spiracular plates (Fig. 11C): irregularly subcircular, relatively large, greatest diameter often in antero-posterior plane, longitudinal diameter of spiracular plate considerably larger than longitudinal diameter of sclerite around anal valves; submarginal row of perforations complete. Gnathosoma (Fig. 11D and E): length from palpal apices to posterior dorsal margin of basis capituli 335–340 (337;  $n = 2$ ), width at apices of dorsolateral projections 382–385 (384;  $n = 2$ ); ratio length to width 0.87–0.89 (0.88;  $n = 2$ ). Basis capituli (Fig. 11D and E): dorsally subhexagonal, with long and sharply pointed lateral projections; lacking auriculae ventrally; with two pairs of ventral setae and one pair of posthypostomal setae. Palpi (Fig. 11D and E): elongate, length (segments II–III) 240–245 (242;  $n = 2$ ), maximum width 61–62 (62,  $n = 2$ ), ratio length to width 3.92 ( $n = 2$ ); segment I well developed ventrally, cylindrical, clear suture between segments II and III, segment II longest, narrow proximally and gradually expanding distally, segment III broadly rounded at apex; segment I with one ventral seta, segment II with four dorsal and three ventral setae, segment III with five dorsal and two ventral setae. Hypostome (Fig. 11E): length from apex to level of posthypostomal setae 222–230 (226;  $n = 2$ ), width at narrowest portion 80 ( $n = 2$ ), ratio length to width 2.78–2.87 (2.83;  $n = 2$ ); club-shaped; dental formula of approximately 5 rows of larger

denticles distally 3/3, formula of approximately 3–4 rows proximally 2/2; 3/3 portion of hypostome comprises slightly more than 1/2 of its total length (ratio avg. 2.5). Coxae (Fig. 11F): coxa I with relatively long internal and external spurs; internal spur slightly shorter than external; both spurs triangular with bluntly tapering apices; external spur on coxae II–IV relatively large, triangular with bluntly tapering apices; size of external spurs slightly decreasing from coxa II to coxa IV; coxa II with short triangular internal spur; spur on coxa IV either not protruding or slightly protruding beyond posterior coxal margin; coxal “pores” (openings of dermal glands or sensilla usually situated close to mid-lateral margin of coxae) present only on coxae I. Genu IV: length 245–255 (250;  $n = 2$ ), width 100 ( $n = 2$ ), ratio length to width 2.45–2.55 (2.50;  $n = 2$ ).

**Larva.** (Fig. 12). Idiosoma: suboval, widest at level of coxae III. Scutum (Fig. 12A): length 330 ( $n = 1$ ), width 440–450 (445;  $n = 2$ ), ratio length to width 0.73 ( $n = 1$ ); pentagonal, posterior margin broadly rounded, posterolateral marginal depressions slight; cervical grooves as faint, shallow depressions. Eyes suboval, slightly bulging, located on lateral margins of scutum at posterior third of scutum length; length of scutum portion posterior to eyes 90–100 (95;  $n = 2$ ), ratio of scutum length to length of its portion posterior to eyes 3.30 ( $n = 1$ ). Setae 3 pairs,  $Sc_2$  25 ( $n = 1$ ),  $Sc_3$  20 ( $n = 2$ ). Dorsal setae of alloscutum 10 pairs; 2 pairs of central dorsals,  $Cd_1$  17 ( $n = 1$ ),  $Cd_2$  18 ( $n = 1$ ); 8 pairs of marginal dorsals,  $Md_1$  23 ( $n = 1$ ),  $Md_8$  20 ( $n = 1$ ). Ventral setae 14 pairs plus 1 pair on anal valves; 3 pairs of sternals,  $St_1$  36 ( $n = 1$ ); 2 pairs of preanals,  $Pa_1$  25 ( $n = 1$ ),  $Pa_2$  25 ( $n = 1$ ); 4 pairs of premarginals,  $Pm_1$  33 ( $n = 1$ ); 5 pairs of marginal ventrals,  $Mv_1$  30 ( $n = 1$ ),  $Mv_5$  24 ( $n = 1$ ). Gnathosoma (Fig. 12B–D): length from palpal apices to posterior dorsal margin of basis capituli 190 ( $n = 1$ ), width at apices of dorsolateral projections 177–202 (190;  $n = 2$ ); ratio length to width 0.94 ( $n = 1$ ). Basis capituli (Fig. 12B–D): dorsally subhexagonal, with relatively short and tapering lateral projections; ventrally rectangular; anterior angle of basis capituli either right or slightly obtuse; auriculae indistinct. Posthypostomal setae 1 pair. Palpi (Fig. 12B–D): elongate, length (segments II–III) 112–122 (117;  $n = 2$ ), width 47–54 (51;  $n = 2$ ), ratio length to width 2.28–2.37 (2.32;  $n = 2$ ); segment I well developed ventrally, cylindrical, faint suture between segments II and III, segment III with relatively small denticle ventrally; segment I without setae, segment II with four dorsal and two ventral setae, segment III with five dorsal and one ventral setae. Hypostome (Fig. 12C): length from apex to the level of posthypostomal setae 100–105 (102;  $n = 2$ ), minimal width 27–30 (29;  $n = 2$ ), ratio length to width 3.50–3.64 (3.57;  $n = 2$ ); club-shaped, dental formula 2/2 throughout length, ca. 5 or 6 larger denticles in median files; denticulated portion comprises approximately half of hypostomal length. Coxae (Fig. 12E): coxa I with large triangular spur with tapering apex, coxae II and III each with moderate triangular spurs. Genu I: length 165–177 (171;  $n = 2$ ), width 80 ( $n = 1$ ), ratio length to width 2.22 ( $n = 1$ ).



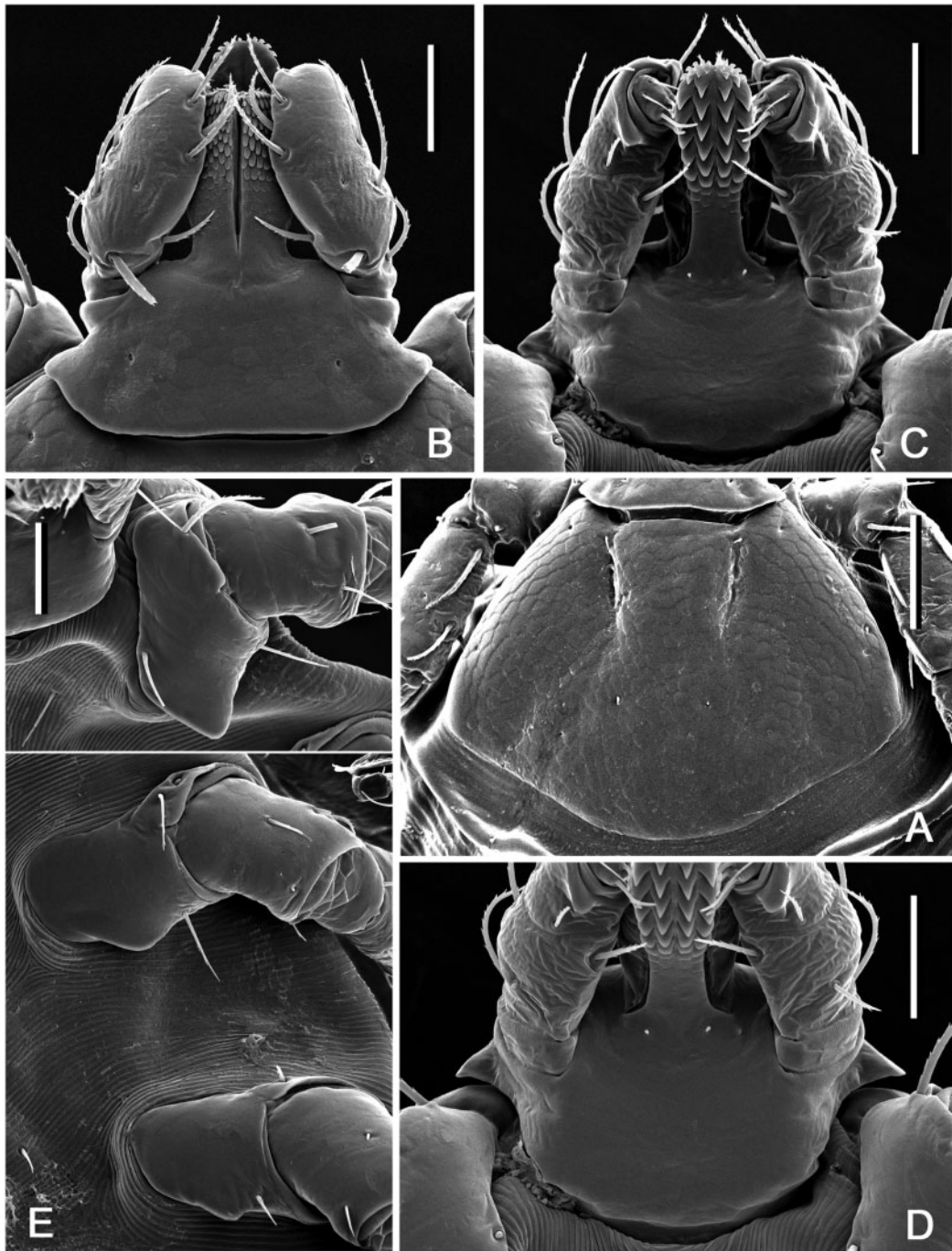
**Fig. 11.** *Dermacentor taiwanensis*, nymph (Taiwan, Taipei, San-chih, Ch'e-ch'eng, USNMENT 00714094). (A) Scutum. Scale bar = 200  $\mu$ m. (B) Setae of alloscutum. Scale bar = 10  $\mu$ m. (C) Spiracular plate. Scale bar = 50  $\mu$ m. Arrows show orientation of spiracular plate (a—anterior; d—dorsal). (D) Gnathosoma dorsally. Scale bar = 100  $\mu$ m. (E) Gnathosoma ventrally. Scale bar = 100  $\mu$ m. (F) Coxae. Scale bar = 100  $\mu$ m.

**HOLOTYPE.** Male, from *Sus* sp., Aoshan, Xindian (24° 57' N, 121° 32' E), New Taipei City, Taiwan, collected by Nishiyama; depository unknown. We were unable to determine the current location of the Sugimoto collection and verify the existence of the holotype.

The male of *Dermacentor taiwanensis* was described and illustrated by Sugimoto (1935, 1937). Arthur

(1960), Teng (1978), and Teng and Jiang (1991) reproduced original illustrations from Sugimoto. Wassef and Hoogstraal (1986a) illustrated the female of true *D. taiwanensis* but presented a description that was based on both *D. taiwanensis* and *D. bellulus* specimens.

**Hosts.** The host data for *D. taiwanensis* are summarized in Table 2. Adults have been collected only from wild boar, *Sus scrofa* L. Both nymphs and larvae

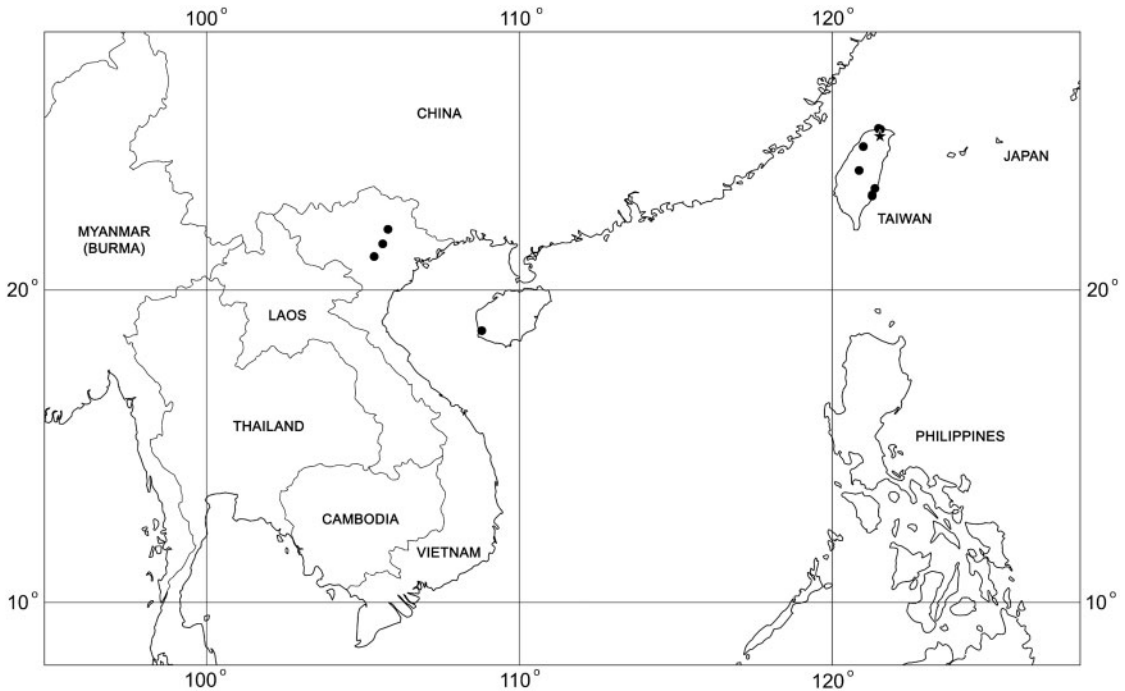


**Fig. 12.** *Dermacentor taiwanensis*, larva (Taiwan, Taipei, San-chih, Ch'e-ch'eng, USNMENT 00714293). (A) Scutum. Scale bar = 100  $\mu$ m. (B) Gnathosoma dorsally. Scale bar = 50  $\mu$ m. (C) Gnathosoma ventrally. Scale bar = 50  $\mu$ m. (D) Gnathosoma anteroventrally. Scale bar = 50  $\mu$ m. (E) Coxae. Scale bar = 50  $\mu$ m.

were collected from greater bandicoot rat, *Bandicota indica* (Bechstein), Pallas's squirrel, *Callosciurus erythraeus* (Pallas), Chinese hare, *Lepus sinensis* Gray, and Chinese ferret-badger, *Melogale moschata* (Gray). Additionally, nymphs were collected from Himalayan striped squirrel, *Tamiops mccllellandii* (Horsfield), rat,

*Rattus* sp., Siberian weasel, *Mustela sibirica* Pallas, and domestic dog.

Adults apparently can be collected throughout the year. In material that we have studied, adult *D. taiwanensis* were collected during all months except March, May, July, and August, with the maximum number of



**Fig. 13.** *Dermacentor taiwanensis*, map of geographical distribution. Star shows type locality, filled circles show confirmed localities.

collections made in February and November. Nymphs of *D. taiwanensis* were collected from May to September, with most collections made in May and July, while few larvae were collected from June to September.

**Distribution.** (Fig. 13). Distribution data for *D. taiwanensis* are summarized in Table 2. The known distribution of this species includes China (Hainan Province), Taiwan (New Taipei, Taipei, and Taitung Counties), and Vietnam (former Bac Thai, Hanoi, and Vinh Phuc Provinces).

Mariana et al. (2005, 2008) and Sun and Xu (2013) recorded *D. taiwanensis* from Malaysia and continental China, respectively. We cannot confirm the identity of this species in these regions and consider such records doubtful and in need of confirmation.

**Etymology.** The specific name is apparently derived from Taiwan, an island and country in East Asia, where the holotype was collected.

**Related Species.** Morphologically, all parasitic stages of *D. bellulus* are quite distinct from those of *D. taiwanensis*.

Males of *D. bellulus* can be distinguished from those of *D. taiwanensis* by the following suite of characters: narrower conscutum with less convex lateral sides (broader conscutum with more convex lateral margins in *D. taiwanensis*); coloration pattern of lateral field: two brown patches, broad anterior and small, often indistinct posterior (one narrow brown line along entire lateral field in *D. taiwanensis*); longer cornua: total length of basis capituli, including cornua, avg. 5.01 cornual length (shorter cornua: total length of basis capituli, including cornua, avg. 6.62 cornual length in

*D. taiwanensis*); shorter and broader palpi: ratio length to width avg. 1.60 (longer and narrower palpi in *D. taiwanensis*: ratio length to width avg. 1.80); longer spurs on coxae I (shorter in *D. taiwanensis*). Females of *D. bellulus* can be distinguished from those of *D. taiwanensis* by the shape of the genital structures: narrowly U-shaped genital aperture, highly bulging preatrial fold, and clearly distinct lateral sclerites in *D. bellulus*, but broadly V-shaped genital aperture, slightly bulging preatrial fold, and indistinct sclerites in *D. taiwanensis*. Additionally, females of *D. bellulus* can be distinguished from those of *D. taiwanensis* by the following suite of characters: narrower scutum: ratio length to width avg. 0.94 (broader scutum: ratio length to width avg. 0.84 in *D. taiwanensis*); longer cornua: total length of basis capituli, including cornua, 8.53 cornual length (shorter cornua: total length of basis capituli, including cornua, 9.07 cornual length in *D. taiwanensis*); broader and shorter palpi: ratio length to width avg. 1.86 (longer and narrower palpi in *D. taiwanensis*: ratio length to width avg. 2.02); longer spurs on coxae I (shorter in *D. taiwanensis*). Nymphs of *D. bellulus* can be distinguished from those of *D. taiwanensis* by the following suite of characters: lateral margins of scutum slightly divergent and subparallel (distinctly divergent in *D. taiwanensis*), eyes situated roughly at 2/3 of scutal length (slightly posterior to mid-length in *D. taiwanensis*), basis capituli subtriangular with long lateral projections (subhexagonal with shorter lateral projections in *D. taiwanensis*), only ca. 1 row of hypostomal denticles with 3/3 formula, all other rows are 2/2 (5 rows, i.e., more than half of hypostome)

length is 3/3 in *D. taiwanensis*), and lacking internal spur on coxae II (small spur in *D. taiwanensis*). Larvae of *D. bellulus* can be distinguished from those of *D. taiwanensis* by the following suite of characters: subtriangular basis capituli with longer and sharper lateral projections dorsally (subhexagonal basis capituli with shorter and more obtuse lateral projections dorsally in *D. taiwanensis*), more pronounced auriculae (indistinct in *D. taiwanensis*), larger denticle on palpal segment III ventrally (smaller in *D. taiwanensis*).

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