Taxonomic revision of the Nearctic *erosa* species group of *Phymata* Latreille, 1802 (Heteroptera: Reduviidae: Phymatinae)

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Abstract

Ambush bugs of the genus *Phymata* Latreille, 1802 (Heteroptera: Reduviidae: Phymatinae) are some of the most recognizable assassin bugs found in North America. Despite their charismatic morphology and ubiquity, the taxonomy of the Nearctic fauna has not been reviewed in more than half a century. Many species are challenging to identify due to their striking intraspecific variation and sexual dimorphism and only subtle interspecific differences. Considering this difficult taxonomy and that recent molecular phylogenetic studies have demonstrated para- or polyphyly among currently recognized species-level taxa, reclassification is required. Ambush bugs of the Nearctic *erosa* species group are herein revised. Eleven previously recognized species are redescribed: *Phymata americana* Melin, 1931; *Phymata arctostaphylae* Van Duzee, 1914; *Phymata borica* Evans, 1931; *Phymata fasciata* (Gray, 1832); *Phymata granulosa* Handlirsch, 1897; *Phymata luteomarginata* Kormilev, 1957; *Phymata pacifica* Evans, 1931; *Phymata pennsylvanica* Handlirsch, 1897; *Phymata rossi* Evans, 1931; *Phymata saileri* Kormilev, 1957; and *Phymata salicis* Cockerell, 1900. Five subspecies are elevated to species rank and redescribed: *Phymata mystica* Evans, 1931 stat. restit.; *Phymata metcalfi* Evans, 1931 stat. restit.; *Phymata mexicana* Melin, 1931 stat. nov.; *Phymata obscura* Kormilev, 1957 stat. nov.; and *Phymata stanfordi* Evans, 1931 stat. nov. One new species from southern California is described: *Phymata paraborica* sp. nov. *Phymata americana coloradensis* Melin, 1931 syn. nov., *Phymata pacifica hainesi* Kormilev, 1962 syn. nov., *Phymata granulosa chiriquiensis* Melin, 1931 syn. nov., and *Phymata granulosa evansi* Kormilev, 1962 syn nov. are each synonymized with their respective nominate subspecies. *Phymata fasciata panamensis* Kormilev, 1962 syn. nov. is synonymized with *Phymata mexicana* Melin, 1931. *Phymata granulosa texasana* Kormilev, 1957 syn. nov., is synonymized with *Phymata rossi*. An illustrated key to ambush bugs of the United States and Canada, detailed diagnoses, habitus images, and distribution maps are provided for all 17 Nearctic *erosa* species group taxa. Furthermore, we incorporate citizen science observations of ambush bugs from an iNaturalist.org project with traditional specimen-based data to expand our knowledge of species-level variation and distribution.

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Introduction

The genus *Phymata* Latreille, 1802 (Heteroptera: Reduviidae) comprises ~110 species of ambush bugs distributed primarily in the New World (Froeschner and Kormilev 1989). Their peculiar morphology, sexual dimorphism, and predation on other flower-associated arthropods have made them popular subjects for evolutionary (Punzalan et al. 2008a; Punzalan et al. 2008b, c, 2010, Weirauch et al. 2011; Punzalan and Rowe 2015, 2016), ecological (Balduf 1941; Mason 1977, 1986; Yong 2005; Masonick et al. 2019), and behavioral research (Dodson and Marshall 1984; Elliott and Elliott 1991, 1994; Yong 2003; Dixon and Rasmussen 2013). While these sit-and-wait predators are easily distinguished from other true bugs by their raptorial forelegs, fusiform antennae, deep antennal excavations of the head and propleura, and dorsolaterally flared pronotum and abdomen, species-level identification within the genus is confounded by subtle interspecific differences, sexual dimorphism, and intraspecific variation. This paradox holds especially true for the Nearctic *erosa* species group, a clade represented by the predominant ambush bug fauna of North America. While the vast majority of *Phymata* found in the wild and in collections belong to just a few common and widespread *erosa* group species, many rare endemic species are found in the deserts and scrublands of the western United States and northern Mexico.

The Nearctic *erosa* group, and *Phymata* as whole, have a convoluted taxonomic history. Taxonomic research on ambush bugs began when Linnaeus in 1758 described the first species, *Cimex erosus*, based on a specimen from Surinam. Latreille erected the genus *Phymata* in 1802 and reclassified *C. erosus* as *Phymata erosa* in 1804, a name under which numerous Neotropical and Nearctic subspecies would later be classified. Handlirsch (1897) provided the first monograph to focus exclusively on Phymatinae, and subsequent revisions

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by Melin (1931), Evans (1931), and Kormilev (1962) further refined understanding of their diversity, and over time, all Nearctic *P. erosa* subspecies were elevated to species rank. In addition to biological issues such as polymorphic traits and sexual dimorphism that hinder species diagnosis, the taxonomy of the *erosa* group has been complicated by the loss or lack of designated types, vague and/or poorly illustrated descriptions, and descriptions based on singleton specimens or on only one sex. What is more, coloration, a feature that can be quite variable within populations and one that changes drastically over time both in live and pinned specimens (Schuh and Slater 1995; Boyle and Start 2020), was used in many cases to define taxa. Outdated descriptions and keys, the most recent having been published in 1962, have culminated in numerous specimens in natural history collections being mis- or unidentified. While little has been done to modernize ambush bug taxonomy, molecular phylogenetics and integrative species delimitation have recently shed light on their species-level relationships and revealed that several *erosa* group taxa are para- or polyphyletic (Masonick et al. 2017; Masonick and Weirauch 2020). Taxonomic updates are sorely needed and insights from these analyses have helped structure the present revision.

The primary aim of this revision is to alleviate confusion pertaining to *erosa* group taxa by providing illustrated keys and detailed species diagnoses. To circumvent the issue of subtle or polymorphic characters and increase the chances of correct identification, our diagnoses reference suites of traits relevant for identifying each taxon, and do not rely on any single attribute. Prior to this project, 11 *erosa* group species and 11 subspecies were known from the Nearctic (Kormilev 1962; Froeschner and Kormilev 1989). Herein, we recognize 17 Nearctic *erosa* species partly through the synonymization or elevation of subspecies to full species of the taxa cataloged by Froeschner and Kormilev. Eleven previously accepted species are redescribed, five subspecies are elevated to species rank and redescribed, and one new species from southern California is described: *Phymata paraborica* sp. nov. *Phymata americana coloradensis* Melin, 1931 syn. nov., *Phymata pacifica hainesi* Kormilev, 1962 syn. nov., *Phymata granulosa chiriquiensis* Melin, 1931 syn. nov., and *Phymata granulosa evansi* Kormilev, 1962 syn. nov. are each synonymized with their respective nominate subspecies. *Phymata fasciata panamensis* Kormilev, 1962 syn. nov. is synonymized with *Phymata mexicana* Melin, 1931. *Phymata granulosa texasana* Kormilev, 1957 syn. nov. is synonymized with *Phymata rossi* Evans, 1931.

Provided in this revision are two illustrated keys to Nearctic ambush bugs. The first (Key$^{(1)}$), covers rare non-*erosa* group *Phymata* native to the United States and Canada. The second (Key$^{(2)}$) deals exclusively with the 17 species of the Nearctic *erosa* group clade. Detailed diagnoses, habitus plates, and distribution maps for these taxa are also included. Our treatment of the Nearctic *erosa* group benefited from the examination of more than 4,125 specimens from 14 natural history collections and survey of 2,290 (as of October 2019) transcontinental citizen science observations from our iNaturalist project "Uncovering the ambush bugs" (https://www.inaturalist.org/projects/uncovering-the-ambush-bugs).

For a list of all *Phymata* known from Canada, the United States, and/or Mexico, see Table 1. Ambush bugs native to North America that are not part of the *erosa* group clade are excluded from this revision. It should be noted that *Phymata severini* Handlirsch, 1897 and *Phymata parva* Handlirsch, 1897 are two taxa from Mexico that were originally erected as subspecies of *P. erosa* and later elevated to species rank by Melin (1931) and Kormilev (1962), respectively. Based on molecular analysis, we found these two species to both be distantly related to the clade of Nearctic ambush bugs treated here (see Masonick and Weirauch, 2020, Figs S3–S6).

Materials & Methods

Specimens, depositories, and databasing: A total of 4,125 databased *erosa* group specimens were examined, of which 1,694 were adult females and 2,385 adult males. Table 2 lists the collections from which material was borrowed and/or is now deposited. Specimens examined are listed by species in the Appendix. We only report material which has been georeferenced: several aberrant individuals which could not be identified or were labeled as being collected drastically out of their known/previously documented range were excluded. We georeferenced older specimens for which geographic coordinates and elevation had not been recorded with locality information using GEOLocate software (https://www.geo-locate.org/) and Google Earth Pro v7.3.2.5776. Specimens were each affixed with a unique specimen identifier (USI) and databased using the Planetary Biodiversity Inventory instance of the Arthropod Easy Capture Database (https://research.amnh.org/pbi/locality/index.php). Specimen information and images can be accessed through the Heteroptera Species Pages (http://research.amnh.org/pbi/heteropteraspeciespage).

Measurements and imaging: Specimen measurements (in mm, Table 3) were taken using a dissecting scope mounted to a digital micrometer positioning system which was connected to a Microcode II® RS-232 digital readout (Boeckeler Instruments®). We recorded measurements of the total body length, the distances across the lateral and posterior pronotal angles (either of which may represent the widest portion of the thorax), and the individual lengths of the pedicel, basiflagellomere, and

Table 1. Checklist of *Phymata* found in Canada, the United States, and/or Mexico.

***erosa* species group clade**	**Non-*erosa* species group taxa**
P. americana Melin, 1931 (CAN, USA, MEX)	*P. albopicta* Handlirsch, 1897 (USA, MEX)
P. arctostaphylae Van Duzee, 1914 (USA, MEX)	*P. annulipes* Stål, 1862 (MEX)
P. borica Evans, 1931 (USA)	*P. barberi* Kormilev, 1962 (MEX)
P. fasciata (Gray, 1832) (USA, MEX)	*P. brailovskyi* Kormilev, 1990 (MEX)
P. granulosa Handlirsch, 1897 (MEX)	*P. luxa* Evans, 1931 (USA, MEX)
P. luteomarginata Kormilev, 1957 (USA)	*P. maculata* Kormilev, 1957 (USA)
P. metcalfi Evans, 1931 stat. restit. (CAN, USA)	*P. noualhieri* Handlirsch, 1897 (USA, MEX)
P. mexicana Melin, 1931 stat. nov. (MEX)	*P. pallida* Kormilev, 1957 (USA)
P. mystica Evans, 1931 stat. restit. (USA)	*P. parva* Handlirsch, 1897 (MEX)
P. obscura Kormilev, 1957 stat. nov. (USA)	*P. rhynocerata* Kormilev, 1957 (MEX)
P. pacifica Evans, 1931 (USA, MEX)	*P. severini* Handlirsch, 1897 (MEX)
P. paraborica sp. nov. (USA)	*P. turnbowi* Kormilev, 1983 (MEX)
P. pennsylvanica Handlirsch, 1897 (CAN, USA)	*P. vicina* Handlirsch, 1897 (CAN, USA)
P. rossi Evans, 1931 (USA)	
P. saileri Kormilev, 1957 (USA)	
P. salicis Cockerell, 1900 (USA)	
P. stanfordi Evans, 1931 stat. nov. (USA)	

distiflagellomere (of the left antenna for all specimens in which it was intact). The ratio of the length of the distiflagellomere to that of the pedicel + basiflagellomere is reported for each taxon. This was calculated by taking the mean across ratios for individual specimens of a given sex. While past taxonomists who dealt with this genus often recorded the maximal width of the abdomen, we omitted this trait from study because it is rather contextual and strongly influenced by how the specimen died and whether it had recently fed and/or was carrying mature eggs. Specimen photographs were taken using a Leica Microsystems imaging system (LAS software v4.3.0), stacked with Zerene Stacker v1.04 to create composite images, and then edited in Adobe Photoshop® CC 2017. Figures were prepared in Adobe Illustrator® CC 2017.

Distribution maps and citizen science data: Specimen-associated locality data and observational data (i.e., geocoordinates and images) shared by the general public with our iNaturalist project "Uncovering the ambush bugs" (https://www.inaturalist.org/projects/uncovering-the-ambush-bugs) were used in conjunction to create more complete estimates of current taxon distributions (data last accessed October 9, 2019). This data is provided in a supplementary spreadsheet (iNaturalist_observations.xlsx) and image archive (iNaturalist_images.zip). Distribution maps (Maps 1-17) were generated with the available coordinate data for each *erosa* group species in SimpleMappr (https://www.simplemappr.net/).

Taxonomic descriptions: Descriptions were partially produced using a WinClada v1.61 (Nixon 1999) based character matrix and then manually edited to accommodate variability and any unique traits for each species. Outlines displaying the consensus pronotal shape were generated following the geometric morphometric approach outlined in Masonick and Weirauch (2020) and are included for each sex in all taxon plates. The curvature of the pronotal lobes are best viewed from a dorsolateral perspective with the lateral margin placed roughly perpendicular to the optical axis. Pronotal shape variation is described from this position unless otherwise noted. Adult males are described in their entirety, but for females, only sexually dimorphic traits are described. Based on combined molecular data, we recently showed that the *erosa* group likely comprises three main species complexes, the *americana*, *borica*, and *fasciata* species complexes (see Masonick and Weirauch, 2020, Fig. 3). While these complexes are fairly well-defined using DNA, no morphological synapomorphies are apparent. Due to the lack of diagnostic characters, we only provide a general description for all *erosa* group taxa and not the individual species complexes themselves. Species descriptions are each accompanied with a plate highlighting their key diagnostic characters. Given their morphological variability and the fact that both age and diet influence color pattern traits in adults (see Punzalan et al. 2008a), we strongly recommend that readers assess multiple characters when making identifications.

Terminology and abbreviations: Anatomical terminology roughly follows that used in Kormilev's (1962) revision of the genus. Morphological features of *Phymata* are illustrated in Figures 1, 2, and 20R. The

following abbreviations are included in keys, plates, and/or text: **aa**, anterior angle; **af**, antennal furrow; **apd**, anterior pronotal disk; **apl**, anterior pronotal lobe; **bflg**, basiflagellomere; **cas2–7**, connexiva of abdominal segments 2–7; **dflg**, distiflagellomere; **fcx**, forecoxa; **ffm**, forefemur; **fp**, frontal process; **ftb**, foretibia; **gp**, granulation patch; **la**, lateral angle; **lc**, longitudinal carina; **ln**, lateral notch; **mspl**, mesopleuron; **mtpl**, metapleuron; **op**, ocellar process; **pa**, posterior angle; **pd**, pedicel; **pop**, preocellar process; **pp**, posterior process; **ppd**, posterior pronotal disk; **ppl**, posterior pronotal lobe; **prpl**, propleuron; **py**, pygophore; **sc**, scutellum; **sppl**, shoulder of the posterior pronotal lobe; **tb**, transverse band of the corium; **tlc**, tubercles of longitudinal carina.

Botanical taxonomy: Plant names and authors listed in this revision are based on the Integrated Taxonomic Information System database (itis.gov).

Nomenclature: The nomenclatural acts contained within this work have been registered in ZooBank (http://www.zoobank.org), the official registry of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:2E2263AA-F7B4-46B6-A26B-97A9F9CE3628.

Table 2. List of specimen depositories and their collection codes.

Collection	Location	Code
American Museum of Natural History	New York City, NY USA	AMNH
California Academy of Sciences	San Francisco, CA USA	CAS
Illinois Natural History Survey Insect Collection	Champaign, IL USA	INHS
University of Kansas Snow Entomological Museum	Lawrence, KS USA	KU
Natural History Museum of Los Angeles County	Los Angeles, CA USA	LACM
Museum of Northern Arizona	Flagstaff, AZ USA	MNA
Montana State University Montana Entomology Collection	Bozeman, MT USA	MTEC
Natural History Museum Vienna	Vienna, Austria	NHMW
Swedish Museum of Natural History	Stockholm, Sweden	NRM
San Diego Natural History Museum	San Diego, CA USA	SDNHM
University of California Riverside Entomology Research Museum	Riverside, CA USA	UCR
Universidad Autonoma de Mexico Instituto de Biologia	Mexico City, Mexico	UNAM
United States National Museum of Natural History	District of Colombia, USA	USNM
University of Idaho William F. Barr Entomological Museum	Moscow, ID USA	WFBM

Table 3. Measurements in mm of *erosa* group taxa. Abbreviations: **body**, total body length; **pd**, pedicel; **bflg**, basiflagellomere; **dflg**, distiflagellomere; **la**, lateral angle of pronotum; **pa**, posterior angle of pronotum.

		Length					Width	
Species		body	pd	bflg	dflg	dflg: pd+bflg	la	pa
Phymata americana								
males (N=8)	**Mean**	**8.81**	**0.62**	**0.66**	**1.15**	**0.89**	**3.37**	**3.42**
	SD	0.30	0.06	0.02	0.09		0.18	0.20
	Range	1.00	0.16	0.07	0.25		0.59	0.48
	Min.	8.15	0.56	0.64	1.05		3.08	3.17
	Max.	9.15	0.72	0.71	1.30		3.67	3.65
females (N=8)	**Mean**	**10.06**	**0.65**	**0.70**	**1.03**	**0.76**	**3.74**	**3.86**
	SD	0.42	0.04	0.07	0.09		0.33	0.21
	Range	1.14	0.11	0.22	0.23		0.93	0.64
	Min.	9.59	0.59	0.54	0.92		3.38	3.63
	Max.	10.73	0.70	0.76	1.14		4.31	4.27
Phymata arctostaphylae								
males (N=5)	**Mean**	**8.08**	**0.56**	**0.63**	**1.23**	**1.04**	**3.40**	**3.30**
	SD	0.41	0.03	0.01	0.05		0.23	0.19
	Range	0.91	0.07	0.02	0.11		0.59	0.51
	Min.	7.70	0.52	0.62	1.18		3.06	3.05
	Max.	8.61	0.59	0.64	1.29		3.65	3.56
females (N=5)	**Mean**	**9.47**	**0.62**	**0.68**	**1.02**	**0.78**	**3.73**	**3.71**
	SD	0.46	0.04	0.05	0.10		0.27	0.23
	Range	1.18	0.11	0.13	0.27		0.66	0.58
	Min.	8.96	0.57	0.64	0.92		3.43	3.40
	Max.	10.14	0.68	0.76	1.20		4.09	3.97
Phymata borica								
males (N=4)	**Mean**	**7.31**	**0.51**	**0.59**	**1.03**	**0.95**	**2.61**	**2.64**
	SD	0.38	0.04	0.06	0.09		0.04	0.05
	Range	0.76	0.10	0.14	0.20		0.08	0.12
	Min.	6.93	0.46	0.52	0.91		2.56	2.57
	Max.	7.69	0.56	0.66	1.11		2.65	2.69
females (N=3)	**Mean**	**8.40**	**0.55**	**0.62**	**0.91**	**0.78**	**2.99**	**2.99**
	SD	0.22	0.05	0.02	0.01		0.09	0.09
	Range	0.43	0.09	0.04	0.02		0.18	0.17
	Min.	8.19	0.52	0.60	0.91		2.89	2.90
	Max.	8.62	0.61	0.64	0.92		3.07	3.07
Phymata fasciata								
males (N=6)	**Mean**	**8.21**	**0.56**	**0.65**	**1.08**	**0.89**	**3.14**	**3.24**
	SD	0.49	0.03	0.03	0.06		0.15	0.18
	Range	1.46	0.07	0.09	0.14		0.43	0.44
	Min.	7.61	0.53	0.61	1.01		2.97	3.07
	Max.	9.07	0.60	0.70	1.15		3.40	3.51
females (N=4)	**Mean**	**9.18**	**0.58**	**0.69**	**0.89**	**0.7**	**3.45**	**3.60**
	SD	0.47	0.08	0.05	0.13		0.22	0.22
	Range	0.98	0.17	0.11	0.27		0.48	0.46
	Min.	8.62	0.52	0.65	0.74		3.25	3.37
	Max.	9.60	0.69	0.76	1.01		3.73	3.83
Phymata granulosa								
males (N=5)	**Mean**	**8.50**	**0.56**	**0.69**	**1.09**	**0.87**	**3.38**	**3.48**
	SD	0.61	0.03	0.04	0.10		0.26	0.26
	Range	1.63	0.08	0.11	0.25		0.61	0.65
	Min.	7.89	0.53	0.65	0.99		3.18	3.25
	Max.	9.52	0.60	0.76	1.24		3.78	3.90
females (N=5)	**Mean**	**9.61**	**0.66**	**0.79**	**1.06**	**0.74**	**3.90**	**4.08**
	SD	0.51	0.05	0.03	0.10		0.28	0.24
	Range	1.22	0.14	0.08	0.23		0.71	0.60
	Min.	8.89	0.59	0.75	0.93		3.57	3.81
	Max.	10.11	0.73	0.83	1.16		4.28	4.42

Species		Length					Width	
		body	pd	bflg	dflg	dflg: pd+bflg	la	pa
Phymata luteomarginata								
males (N=5)	**Mean**	**6.99**	**0.51**	**0.49**	**0.96**	**0.96**	**2.71**	**2.80**
	SD	0.44	0.05	0.05	0.13		0.28	0.27
	Range	1.15	0.12	0.12	0.32		0.72	0.62
	Min.	6.30	0.44	0.46	0.75		2.27	2.37
	Max.	7.45	0.56	0.57	1.06		2.99	2.99
females (N=5)	**Mean**	**7.75**	**0.49**	**0.56**	**0.77**	**0.73**	**2.86**	**2.97**
	SD	0.82	0.06	0.06	0.09		0.25	0.25
	Range	1.99	0.14	0.14	0.19		0.60	0.60
	Min.	6.99	0.42	0.51	0.66		2.63	2.72
	Max.	8.97	0.56	0.64	0.85		3.23	3.32
Phymata metcalfi								
males (N=6)	**Mean**	**7.73**	**0.54**	**0.58**	**0.96**	**0.86**	**3.01**	**3.04**
	SD	0.54	0.03	0.04	0.12		0.30	0.28
	Range	1.34	0.09	0.10	0.30		0.75	0.76
	Min.	7.16	0.51	0.53	0.83		2.68	2.68
	Max.	8.49	0.60	0.63	1.13		3.43	3.43
females (N=6)	**Mean**	**8.53**	**0.55**	**0.61**	**0.82**	**0.71**	**3.23**	**3.27**
	SD	0.68	0.05	0.04	0.07		0.29	0.32
	Range	1.78	0.13	0.12	0.16		0.64	0.80
	Min.	7.47	0.51	0.53	0.74		2.79	2.78
	Max.	9.25	0.64	0.65	0.90		3.44	3.58
Phymata mexicana								
males (N=5)	**Mean**	**8.43**	**0.62**	**0.66**	**1.14**	**0.89**	**3.55**	**3.35**
	SD	0.35	0.02	0.04	0.08		0.29	0.28
	Range	0.88	0.05	0.12	0.18		0.77	0.67
	Min.	8.14	0.59	0.61	1.05		3.29	3.17
	Max.	9.03	0.64	0.73	1.24		4.06	3.84
females (N=5)	**Mean**	**9.40**	**0.64**	**0.73**	**1.00**	**0.73**	**3.88**	**3.76**
	SD	0.26	0.06	0.05	0.09		0.27	0.29
	Range	0.67	0.15	0.11	0.20		0.68	0.78
	Min.	9.12	0.59	0.68	0.91		3.51	3.34
	Max.	9.80	0.73	0.79	1.11		4.19	4.13
Phymata mystica								
males (N=5)	**Mean**	**8.26**	**0.62**	**0.63**	**1.05**	**0.84**	**3.29**	**3.36**
	SD	0.49	0.05	0.05	0.05		0.12	0.17
	Range	1.00	0.12	0.13	0.11		0.27	0.40
	Min.	7.73	0.57	0.57	0.99		3.16	3.14
	Max.	8.72	0.69	0.70	1.10		3.43	3.54
females (N=5)	**Mean**	**9.19**	**0.62**	**0.67**	**0.88**	**0.68**	**3.57**	**3.61**
	SD	0.44	0.05	0.03	0.07		0.16	0.23
	Range	1.05	0.12	0.07	0.15		0.34	0.53
	Min.	8.63	0.56	0.65	0.79		3.40	3.37
	Max.	9.67	0.68	0.71	0.94		3.75	3.90
Phymata obscura								
males (N=4)	**Mean**	**8.35**	**0.57**	**0.63**	**1.05**	**0.87**	**3.23**	**3.21**
	SD	0.58	0.05	0.04	0.07		0.32	0.29
	Range	1.31	0.11	0.10	0.18		0.76	0.71
	Min.	7.57	0.51	0.58	0.95		2.90	2.85
	Max.	8.88	0.62	0.68	1.13		3.66	3.56
females (N=4)	**Mean**	**9.93**	**0.61**	**0.68**	**1.00**	**0.77**	**3.66**	**3.79**
	SD	0.33	0.04	0.04	0.08		0.35	0.34
	Range	0.79	0.10	0.09	0.18		0.84	0.82
	Min.	9.52	0.56	0.65	0.89		3.31	3.44
	Max.	10.31	0.66	0.74	1.07		4.16	4.26

Species		Length					Width	
		body	pd	bflg	dflg	dflg: pd+bflg	la	pa
Phymata pacifica								
males (N=5)	**Mean**	**6.60**	**0.46**	**0.56**	**0.82**	**0.81**	**2.66**	**2.53**
	SD	0.17	0.04	0.04	0.04		0.08	0.07
	Range	0.36	0.09	0.09	0.10		0.18	0.15
	Min.	6.40	0.43	0.51	0.77		2.57	2.46
	Max.	6.76	0.52	0.60	0.87		2.75	2.61
females (N=5)	**Mean**	**7.85**	**0.52**	**0.63**	**0.70**	**0.61**	**3.17**	**3.05**
	SD	0.58	0.07	0.04	0.06		0.20	0.17
	Range	1.59	0.18	0.08	0.13		0.44	0.38
	Min.	7.18	0.44	0.60	0.63		2.96	2.88
	Max.	8.77	0.61	0.68	0.76		3.40	3.26
Phymata paraborica								
males (N=8)	**Mean**	**6.84**	**0.52**	**0.54**	**0.90**	**0.86**	**2.54**	**2.54**
	SD	0.18	0.03	0.03	0.05		0.09	0.09
	Range	0.56	0.08	0.08	0.13		0.28	0.28
	Min.	6.59	0.48	0.50	0.84		2.38	2.40
	Max.	7.15	0.56	0.57	0.97		2.66	2.69
females (N=8)	**Mean**	**7.42**	**0.52**	**0.55**	**0.74**	**0.69**	**2.71**	**2.70**
	SD	0.32	0.05	0.02	0.04		0.13	0.13
	Range	1.05	0.11	0.08	0.12		0.42	0.35
	Min.	6.89	0.46	0.51	0.65		2.47	2.52
	Max.	7.94	0.56	0.59	0.78		2.88	2.87
Phymata pennsylvanica								
males (N=5)	**Mean**	**8.19**	**0.56**	**0.59**	**1.32**	**1.15**	**2.92**	**2.96**
	SD	0.35	0.02	0.06	0.10		0.14	0.18
	Range	0.94	0.05	0.16	0.25		0.34	0.47
	Min.	7.73	0.53	0.52	1.15		2.75	2.73
	Max.	8.67	0.58	0.68	1.41		3.09	3.20
females (N=5)	**Mean**	**9.27**	**0.57**	**0.63**	**1.04**	**0.88**	**3.27**	**3.36**
	SD	0.22	0.05	0.09	0.04		0.13	0.17
	Range	0.58	0.13	0.26	0.10		0.35	0.45
	Min.	8.97	0.51	0.50	1.01		3.16	3.20
	Max.	9.55	0.63	0.76	1.11		3.50	3.65
Phymata rossi								
males (N=3)	**Mean**	**7.47**	**0.57**	**0.59**	**1.01**	**0.87**	**2.90**	**2.88**
	SD	0.77	0.07	0.04	0.03		0.29	0.24
	Range	1.41	0.14	0.07	0.05		0.58	0.47
	Min.	6.59	0.52	0.57	0.98		2.61	2.61
	Max.	8.00	0.65	0.64	1.03		3.18	3.08
females (N=3)	**Mean**	**8.52**	**0.59**	**0.64**	**0.87**	**0.71**	**3.21**	**3.28**
	SD	0.31	0.07	0.02	0.04		0.14	0.19
	Range	0.62	0.14	0.03	0.07		0.25	0.37
	Min.	8.21	0.51	0.62	0.83		3.12	3.11
	Max.	8.82	0.65	0.66	0.90		3.38	3.48
Phymata saileri								
males (N=1)	**Meas.**	**8.01**	**0.58**	**0.56**	**1.04**	**0.91**	**2.86**	**3.25**
females (N=1)	**Meas.**	**8.08**	**0.51**	**0.55**	**0.8**	**0.75**	**3.03**	**3.30**
Phymata salicis								
males (N=2)	**Mean**	**7.96**	**0.59**	**0.59**	**0.69**	**0.59**	**2.77**	**2.63**
	SD	0.27	0.05	0.07	0.07		0.12	0.02
	Range	0.38	0.07	0.10	0.10		0.17	0.03
	Min.	7.77	0.55	0.54	0.64		2.69	2.62
	Max.	8.15	0.63	0.64	0.74		2.85	2.65
females (N=3)	**Mean**	**8.34**	**0.54**	**0.59**	**0.59**	**0.52**	**2.84**	**2.76**
	SD	0.57	0.03	0.03	0.04		0.18	0.13
	Range	0.99	0.06	0.06	0.07		0.33	0.25
	Min.	8.01	0.51	0.56	0.56		2.71	2.66
	Max.	9.00	0.57	0.62	0.63		3.04	2.91

Species		Length				dflg: pd+bflg	Width	
		body	pd	bflg	dflg		la	pa
Phymata stanfordi								
males (N=5)	**Mean**	**7.59**	**0.55**	**0.58**	**0.96**	**0.84**	**2.77**	**2.81**
	SD	0.39	0.02	0.03	0.05		0.13	0.11
	Range	1.09	0.04	0.08	0.11		0.30	0.26
	Min.	7.03	0.53	0.55	0.90		2.61	2.63
	Max.	8.13	0.57	0.63	1.01		2.92	2.89
females (N=5)	**Mean**	**8.40**	**0.62**	**0.65**	**0.81**	**0.65**	**3.07**	**3.09**
	SD	0.69	0.04	0.06	0.06		0.25	0.27
	Range	1.60	0.09	0.16	0.11		0.64	0.65
	Min.	7.69	0.56	0.58	0.75		2.77	2.77
	Max.	9.29	0.66	0.73	0.86		3.41	3.42

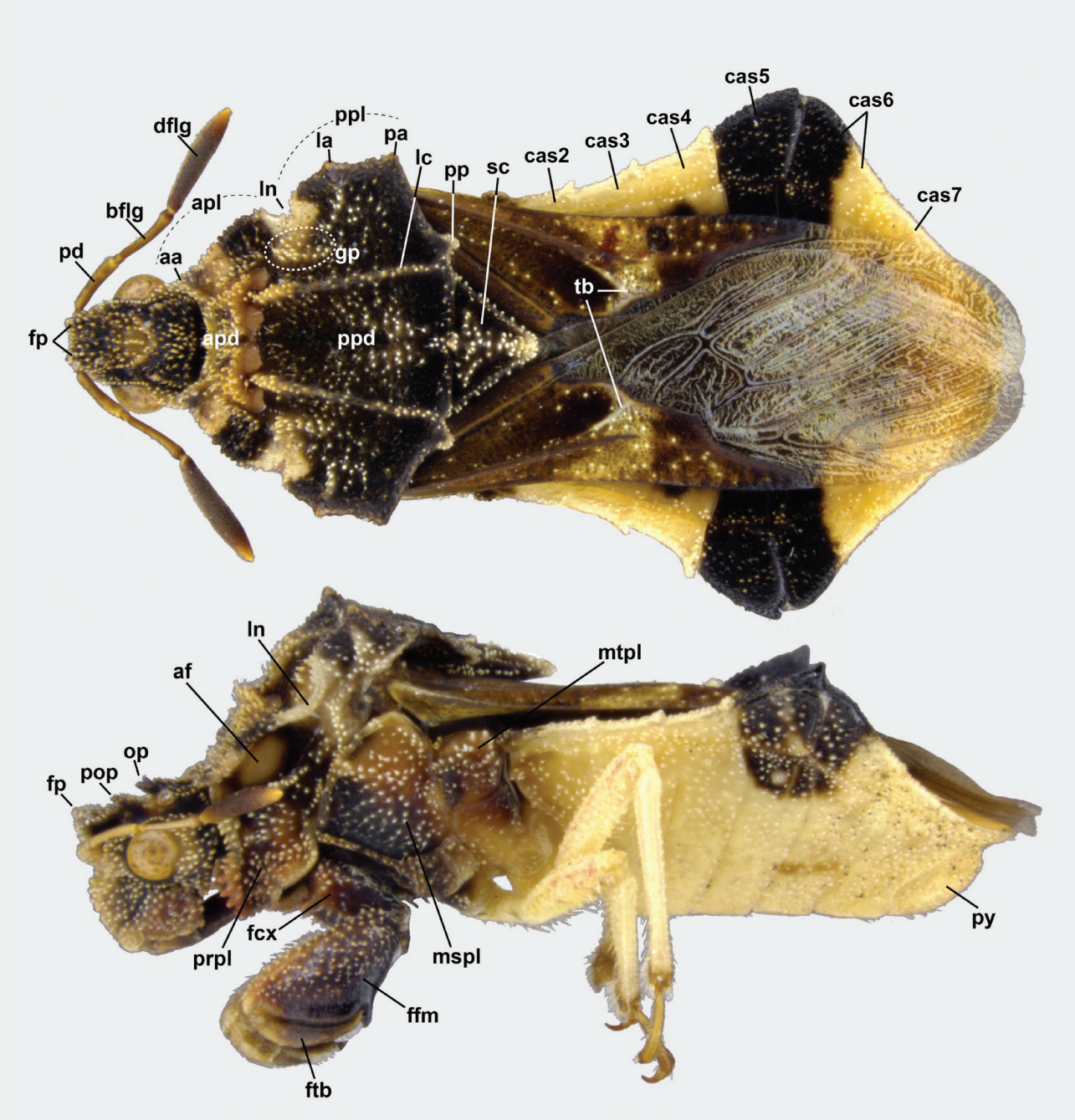


Figure 1. General morphology of Nearctic *erosa* group taxa (*P. granulosa* ♂).
Morphological features are abbreviated as follows: **aa**, anterior angle; **af**, antennal furrow; **apd**, anterior pronotal disk; **apl**, anterior pronotal lobe; **bflg**, basiflagellomere; **cas2–7**, connexiva of abdominal segments 2–7; **dflg**, distiflagellomere; **fcx**, forecoxa; **ffm**, forefemur; **fp**, frontal process; **ftb**, foretibia; **gp**, granulation patch; **la**, lateral angle; **lc**, longitudinal carina; **ln**, lateral notch; **mspl**, mesopleuron; **mtpl**, metapleuron; **op**, ocellar process; **pa**, posterior angle; **pd**, pedicel; **pop**, preocellar process; **pp**, posterior process; **ppd**, posterior pronotal disk; **ppl**, posterior pronotal lobe; **prpl**, propleuron; **py**, pygophore; **sc**, scutellum; **tb**, transverse band of the corium.

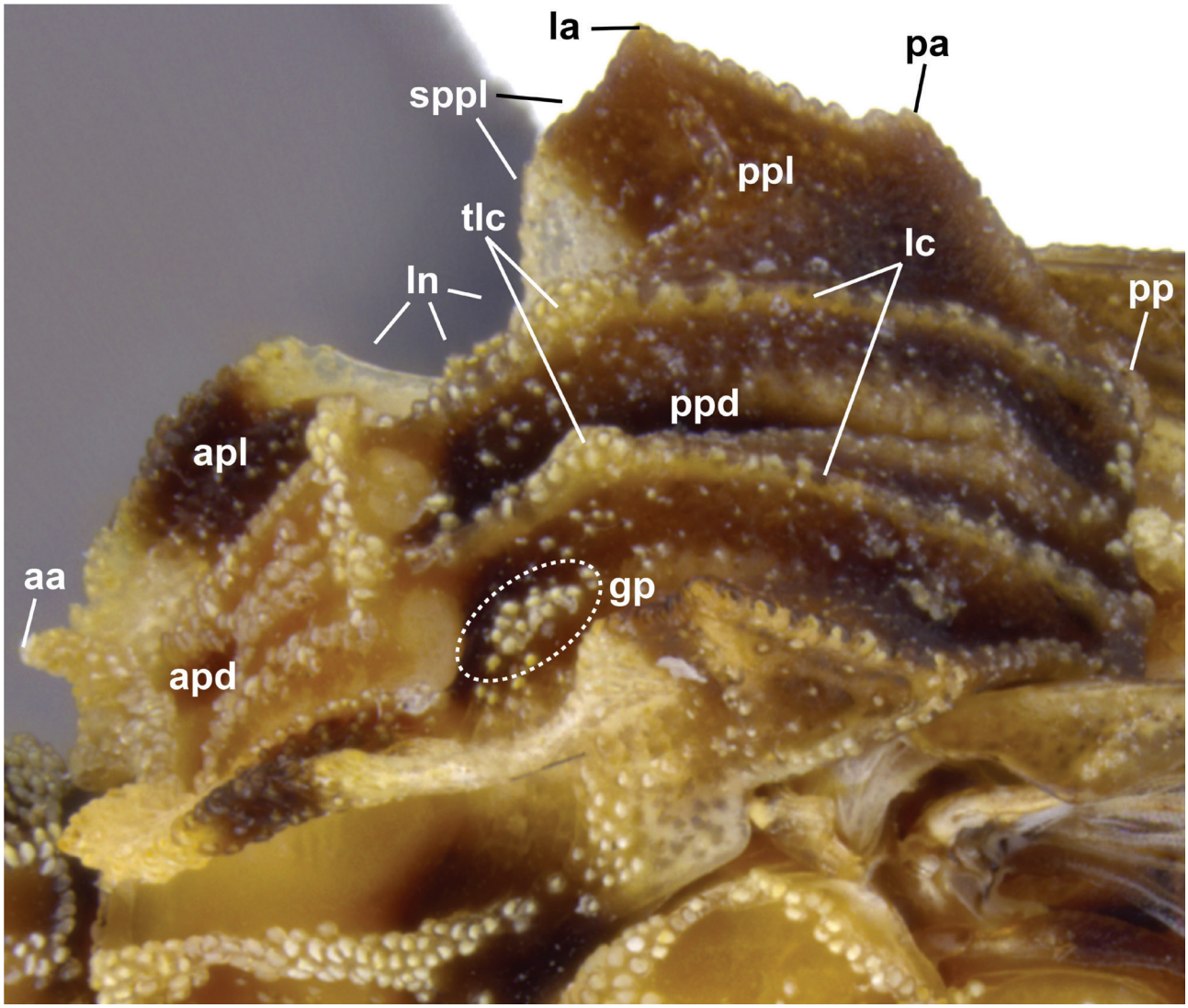
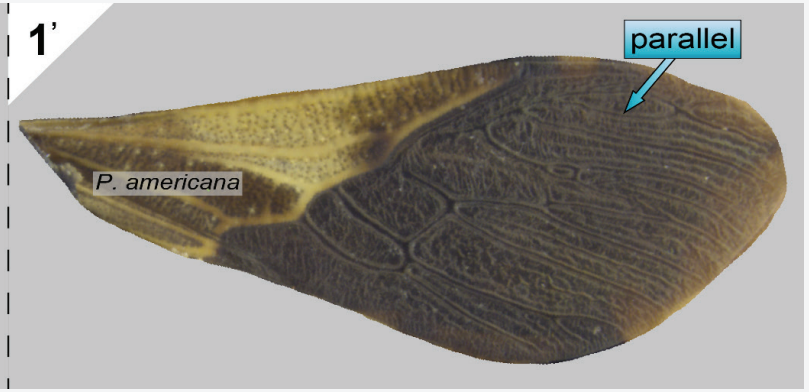
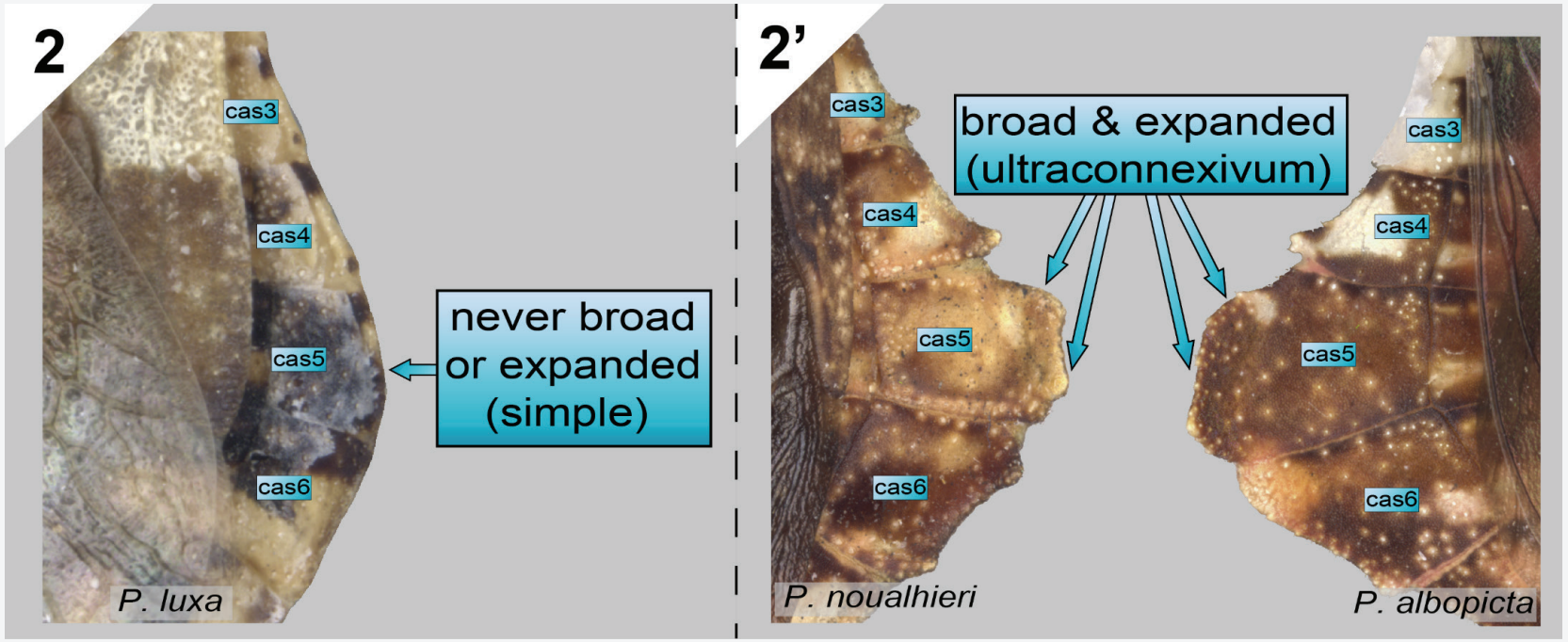


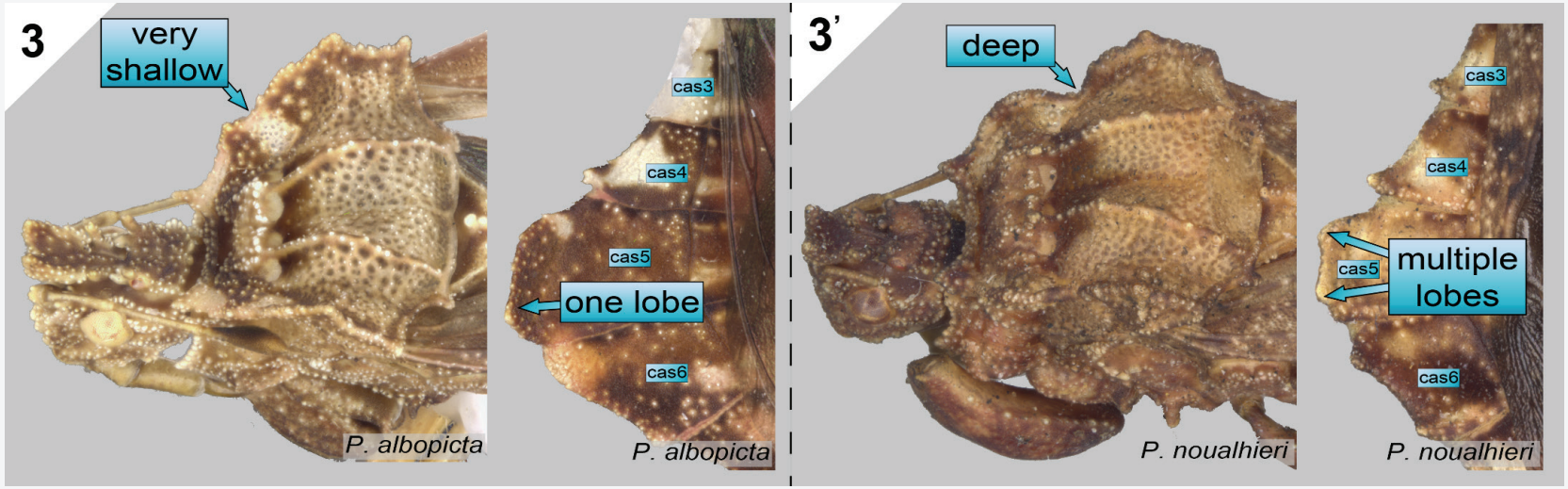
Figure 2. Pronotal morphology from dorsolateral view (*P. fasciata* ♂).
Morphological features are abbreviated as follows: **aa**, anterior angle; **apd**, anterior pronotal disk; **apl**, anterior pronotal lobe; **gp**, granulation patch; **la**, lateral angle; **lc**, longitudinal carina; **ln**, lateral notch; **pa**, posterior angle; **pp**, posterior process; **ppd**, posterior pronotal disk; **ppl**, posterior pronotal lobe; **sppl**, shoulder of the posterior pronotal lobe; **tlc**, tubercles of longitudinal carina.

Key(1) to *Phymata* of the United States and Canada

	
1) Distal portion of forewing membrane with anastomosed veins.	1') Distal portion of forewing membrane with veins mostly parallel, not anastomosed.
2	4



2) Connexivum of abdominal segment 5 never greatly expanded, more or less quadrate; small-sized, length <6 mm, found in the southwestern US and northern Mexico.	2') Connexivum of abdominal segment 5 greatly expanded (forming an ultraconnexivum), not quadrate; small to medium-sized, length >6 mm, found in the southeastern US and throughout Mexico.
Phymata luxa Evans, 1931	3

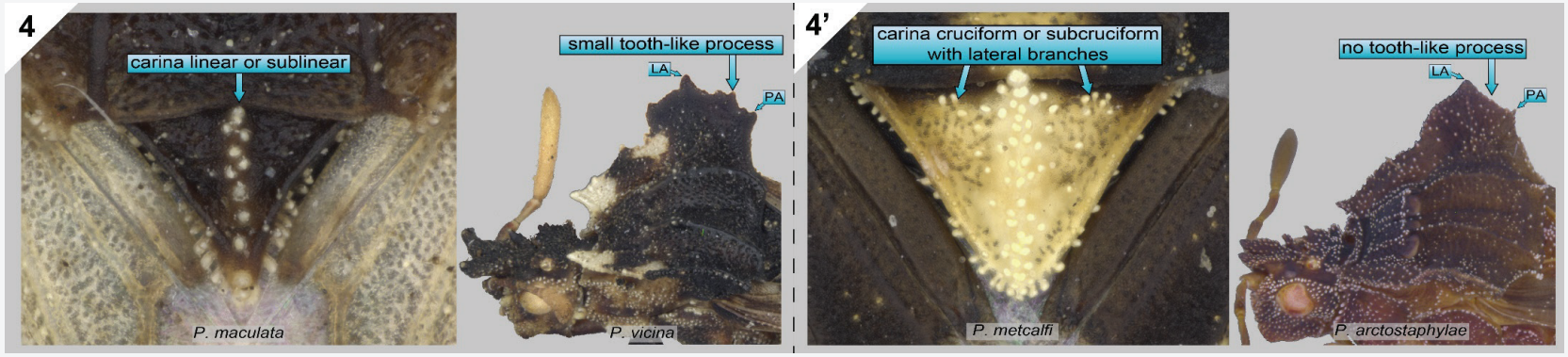


3) Lateral notch absent or very shallow; connexivum of abdominal segment 5 with single lobe.

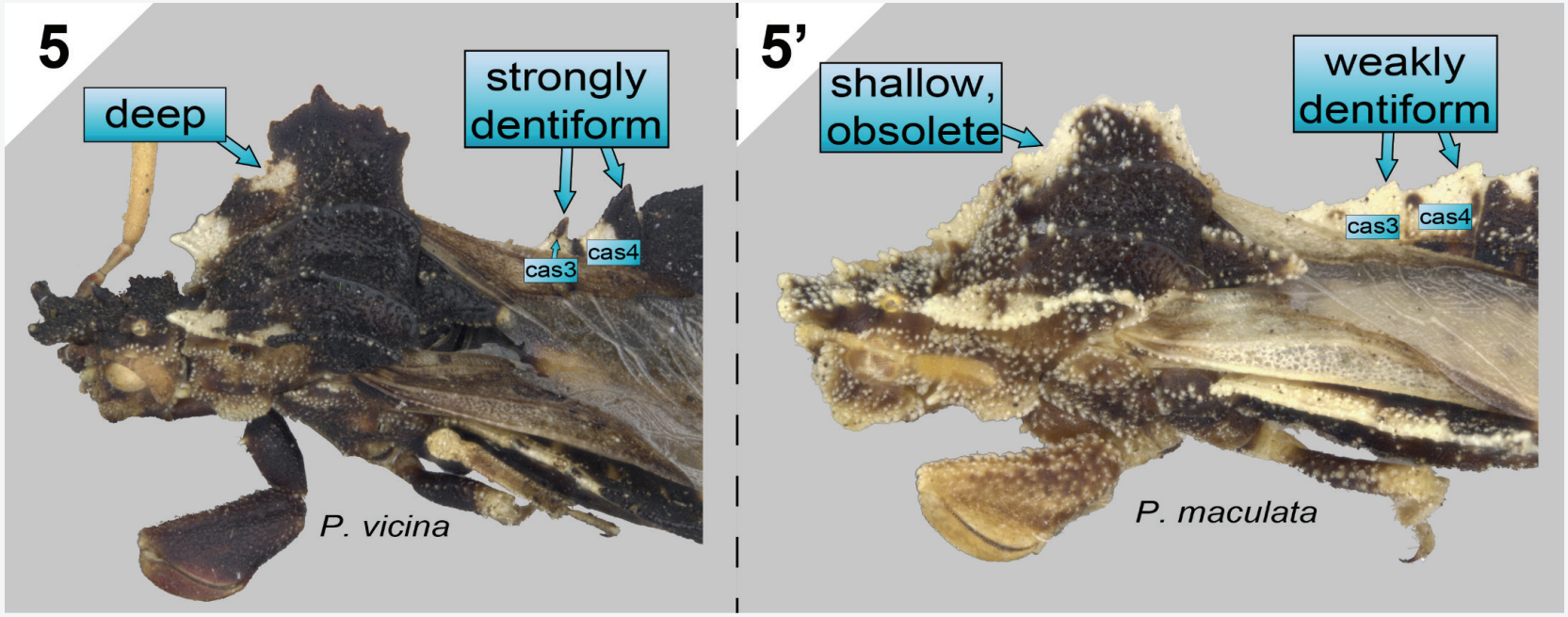
Phymata albopicta Handlirsch, 1897

3') Lateral notch deep; connexivum of abdominal segment 5 with two distinct lobes.

Phymata noualhieri Handlirsch, 1897

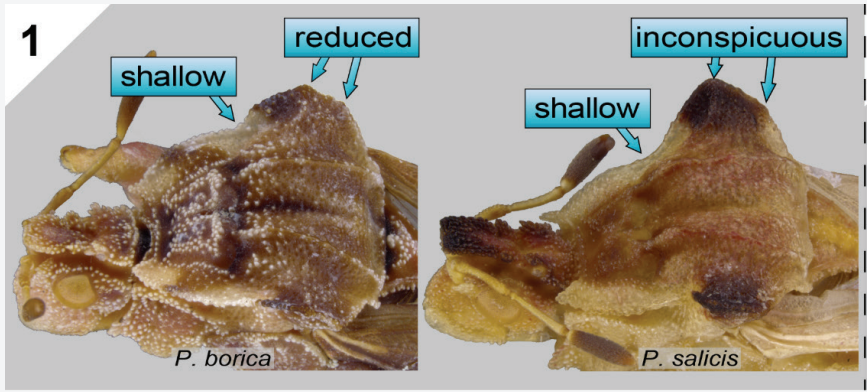


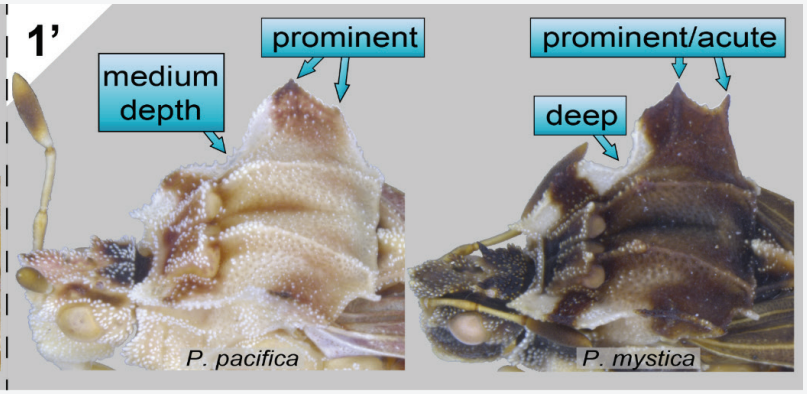
4) Scutellum bearing only a linear or sublinear longitudinal carina; pronotal margin between the lateral and posterior angles usually bearing a small tooth-like process; small-sized, males <~6 mm and females <~6.5 mm in length.	4') Scutellar carinae cruciform or subcruciform with longitudinal carina and lateral branches both usually granulated; pronotal margin between the lateral and posterior angles usually without a tooth-like process; size variable, adults ~6–11 mm in length.
5	*erosa* species group [see key]



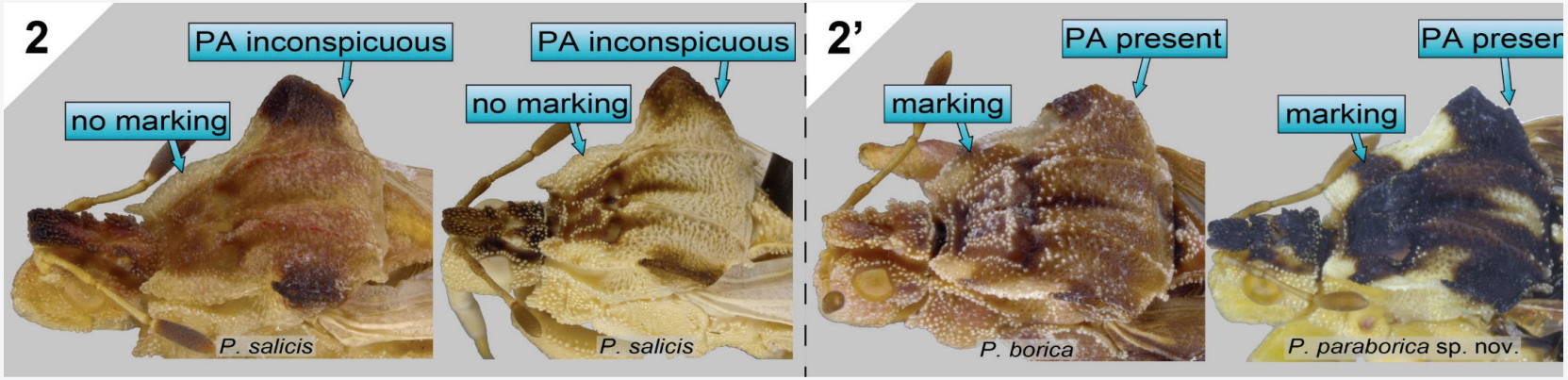
5) Lateral notch of pronotum relatively deep and conspicuous; connexiva strongly dentiform.	5') Lateral notch of pronotum very shallow or obsolete; connexiva weakly dentiform.
Phymata vicina Handlirsch, 1897	*Phymata maculata* Kormilev, 1957 + *Phymata pallida* Kormilev, 1957

Key[(2)] to species of the Nearctic *erosa* species group

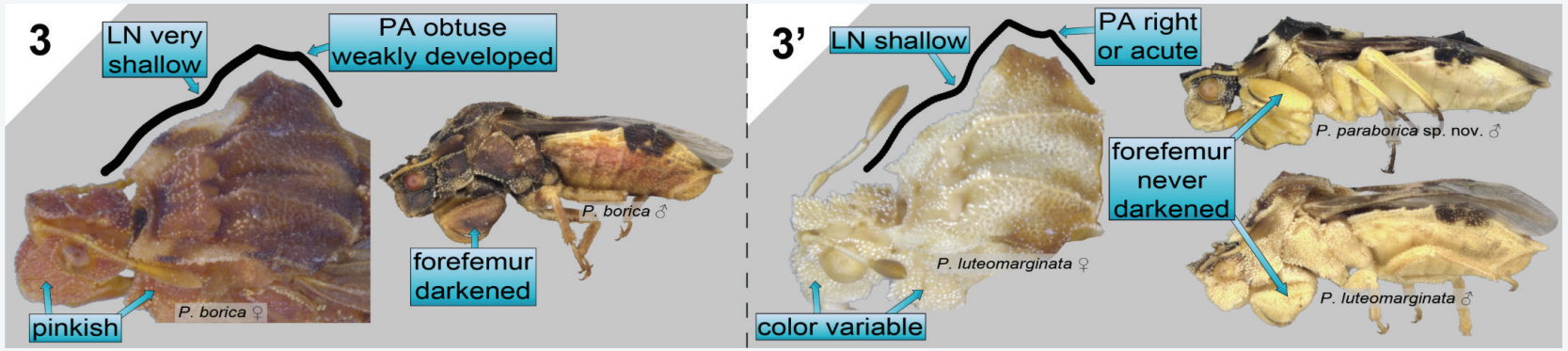




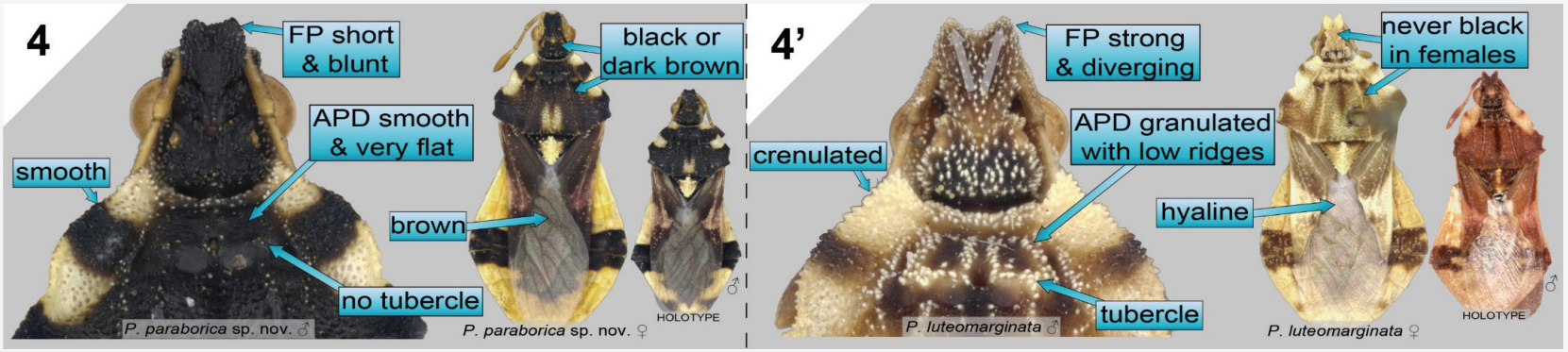
1) Lateral notch shallow; lateral and posterior pronotal angles reduced or inconspicuous.	1') Lateral notch medium to deep; lateral and posterior pronotal angles prominent and often acute.
2	5



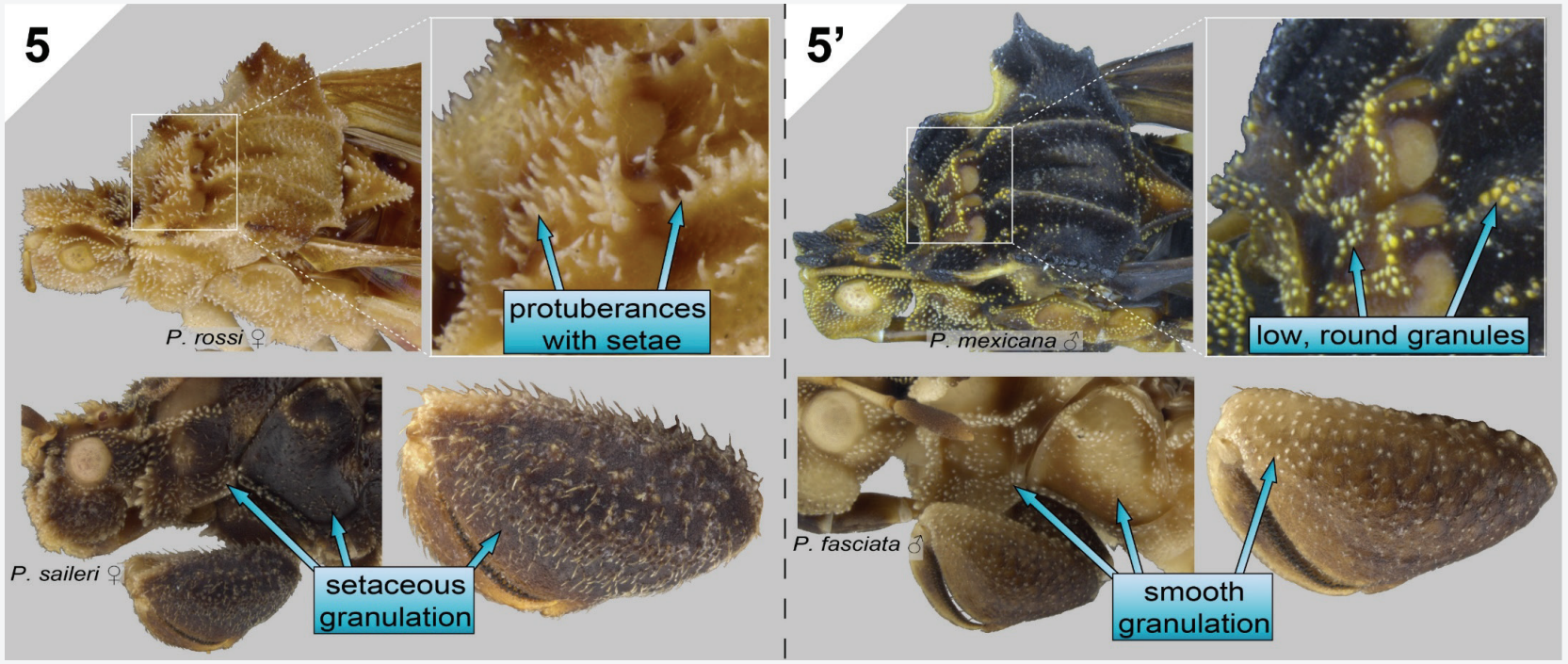
2) Posterior pronotal angle inconspicuous; anterior pronotal lobe never with dark markings laterally; restricted to Arizona, California, and Nevada.	2') Posterior pronotal angle present; anterior pronotal lobe usually with conspicuous dark markings that reach the lateral margin; distribution variable.
Phymata salicis Cockerell, 1900	3



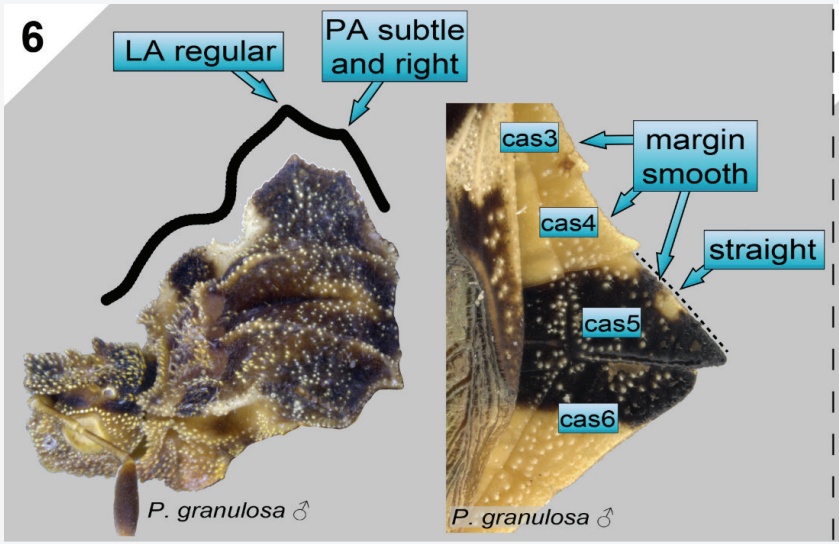
3) Lateral notch extremely shallow; posterior pronotal lobe barely rising above lateral notch; lateral angle obtuse; posterior angle weakly developed, obtuse; frontal process usually short and blunt; granulation patch near lateral notch either absent or diffuse; females usually pinkish to reddish in color; males sometimes with forefemur darkened; found in the Colorado Plateau region of the US.	3') Lateral notch slightly deeper; posterior pronotal lobe rising above lateral notch; lateral angle obtuse in females, right in males; posterior angle more developed, right or acute; frontal process variable; granulation patch near lateral notch either present or diffuse; females variable in color; males never with forefemur darkened; confined to California and Nevada.
Phymata borica Evans, 1931	4

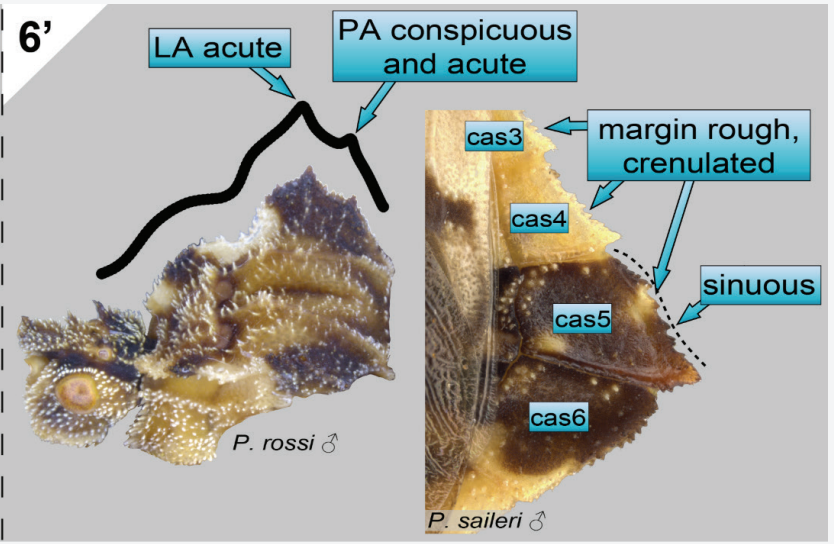


4) Anterior pronotal disk very flat, relatively smooth and without tubercles anterior to transverse sulcus; lateral pronotal margin relatively smooth; frontal process usually very short and blunt; forewing membrane always brown; distiflagellomere of females shorter than or subequal to basiflagellomere; distiflagellomere of males shorter than pedicel + basiflagellomere; anterior margin of pedicel relatively smooth / without granulation; lateral and posterior angles almost always reduced and former usually either right or obtuse; both males and females can exhibit very dark coloration on the head and pronotum; restricted to southern California.	4') Anterior pronotal disk uneven, with small setaceous granules and tubercles anterior to transverse sulcus; lateral pronotal margin rough and crenulated; frontal process variable, often well developed and diverging; forewing membrane usually hyaline; distiflagellomere of females longer than basiflagellomere; distiflagellomere of males subequal to pedicel + basiflagellomere; anterior margin of pedicel lined with granulation (usually more prominent in females); lateral and posterior angles in some northern and desert populations prominent and acute; usually lighter in color than above, especially females; found across southern California's transverse ranges, the Mojave desert, Sierra Nevada mountains and Great Basin region.
Phymata paraborica sp. nov.	*Phymata luteomarginata* Kormilev, 1957

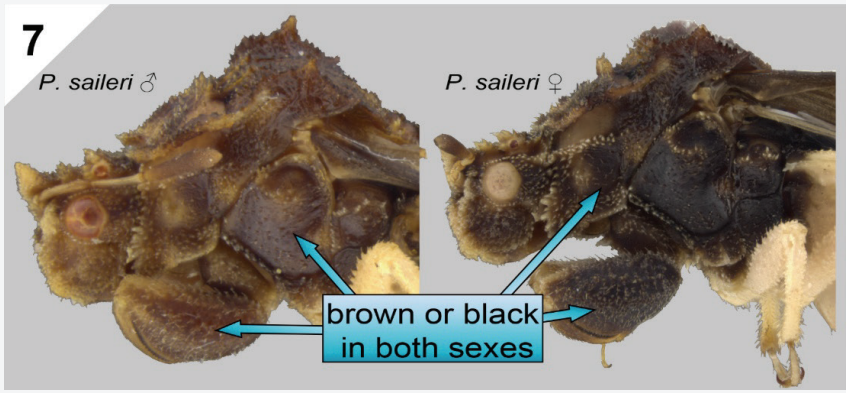


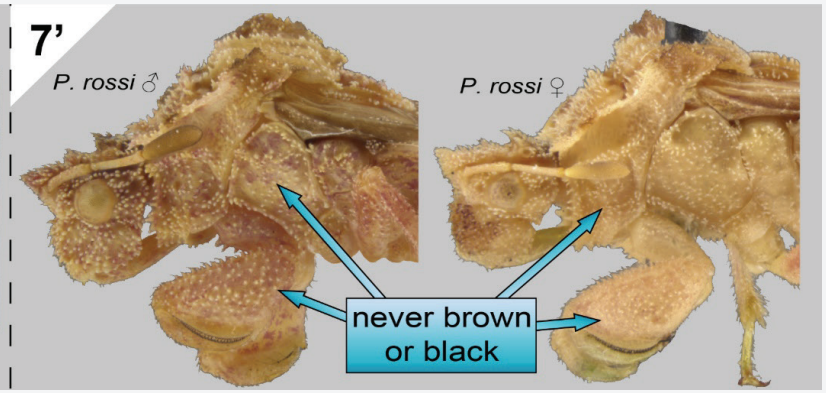
5) Conspicuous setae-bearing protuberances present on pronotal discs, lateral pronotal margin, and surface of forefemur.	5') Conspicuous setae-bearing protuberances absent from pronotal discs, lateral pronotal margin, and surface of forefemur.
6	8



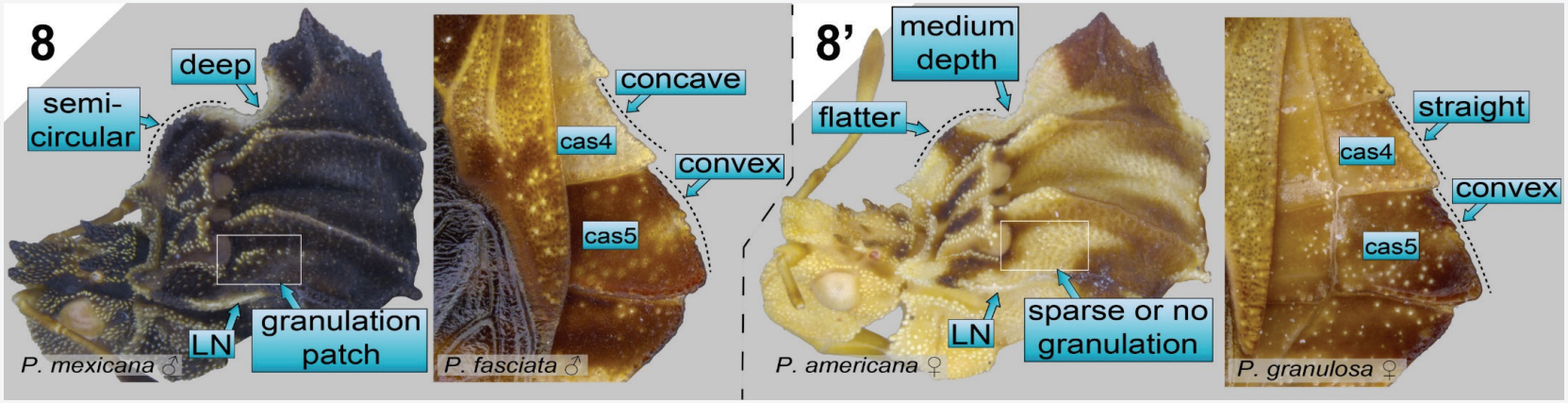


6) Lateral angle regular; posterior pronotal angle less conspicuous, projected dorsad; margin of connexiva of abdominal segments 3–6 relatively smooth; lateral margin of connexivum of abdominal segment 5 usually straight or slightly convex; restricted to Mexico and Central America.	6') Lateral and posterior pronotal angles prominent and dentiform, projected posteriorly; margin of connexiva of abdominal segments 3–6 roughly crenulated; lateral margin of connexivum of abdominal segment 5 usually sinuous; found in the southwestern US.
Phymata granulosa Handlirsch, 1897	7

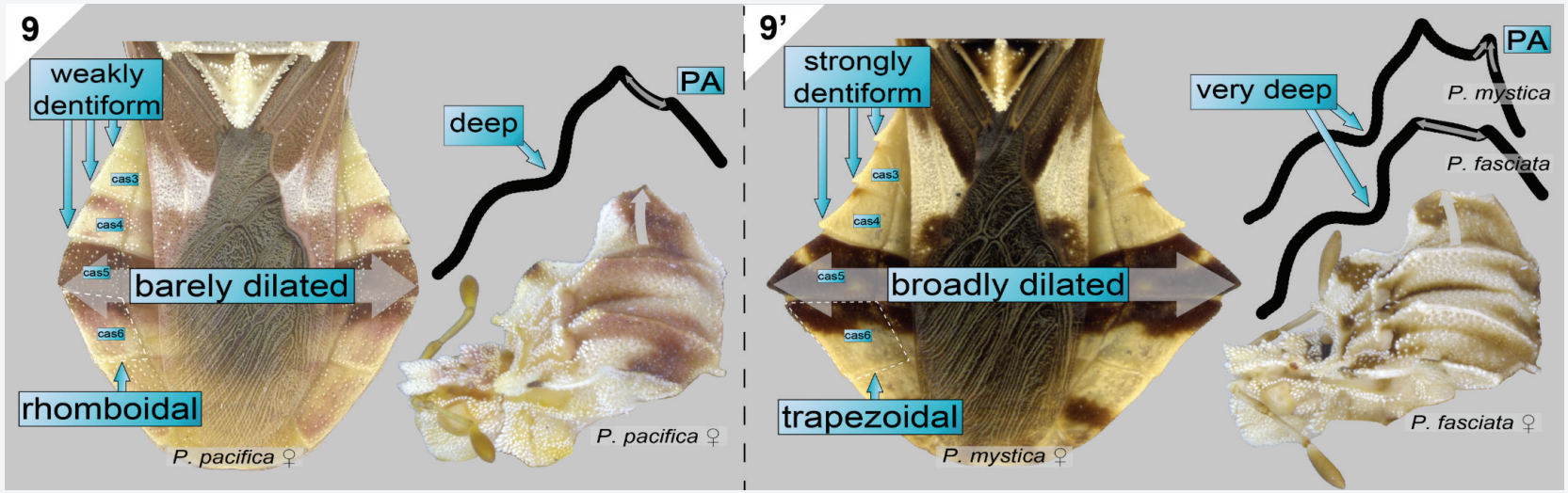




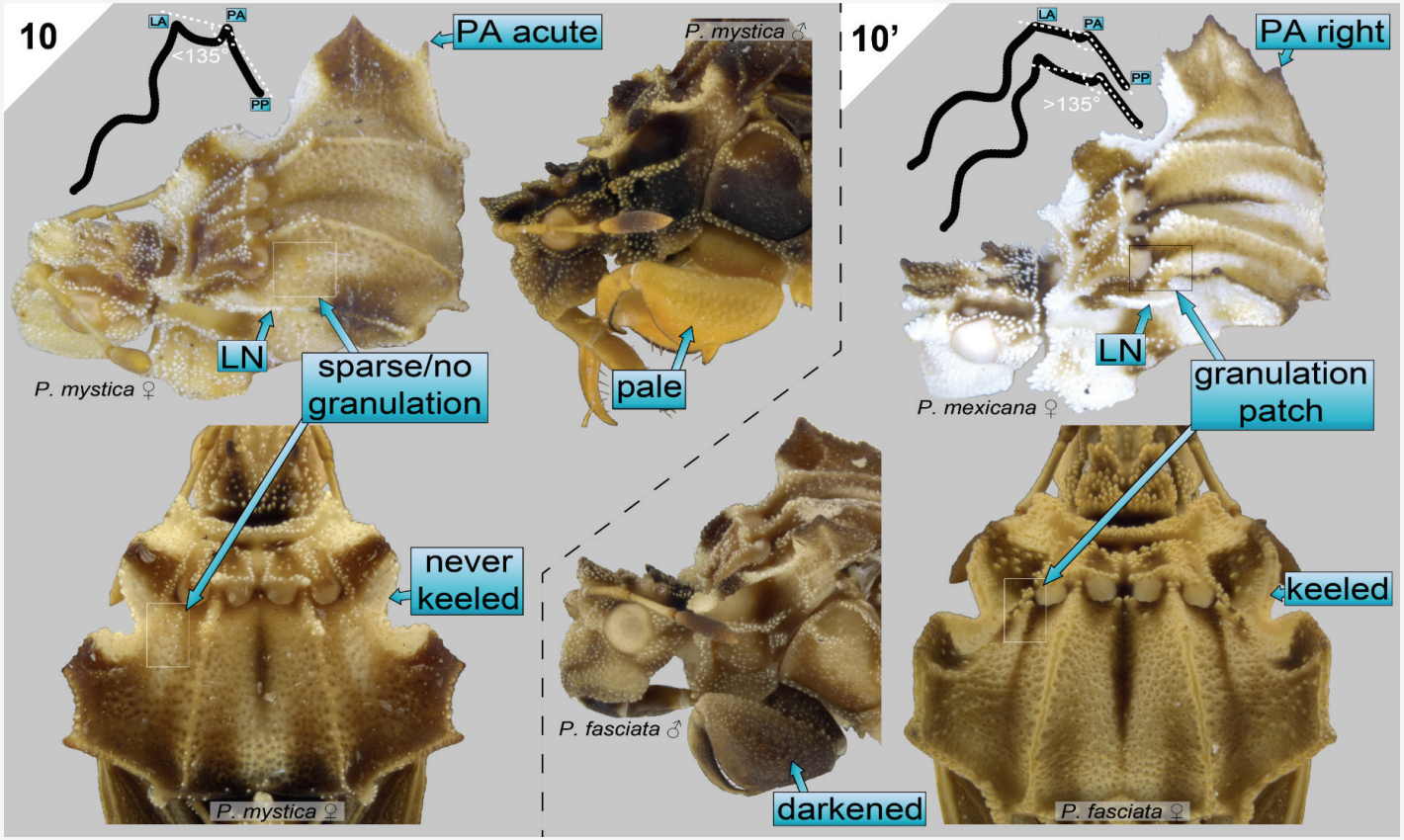
7) Forefemur dark colored in both sexes; dorsal and lateral surface of thorax glossy.	7') Forefemur never dark colored; dorsal and lateral surface of thorax matte.
Phymata saileri Kormilev, 1957	*Phymata rossi* Evans, 1931



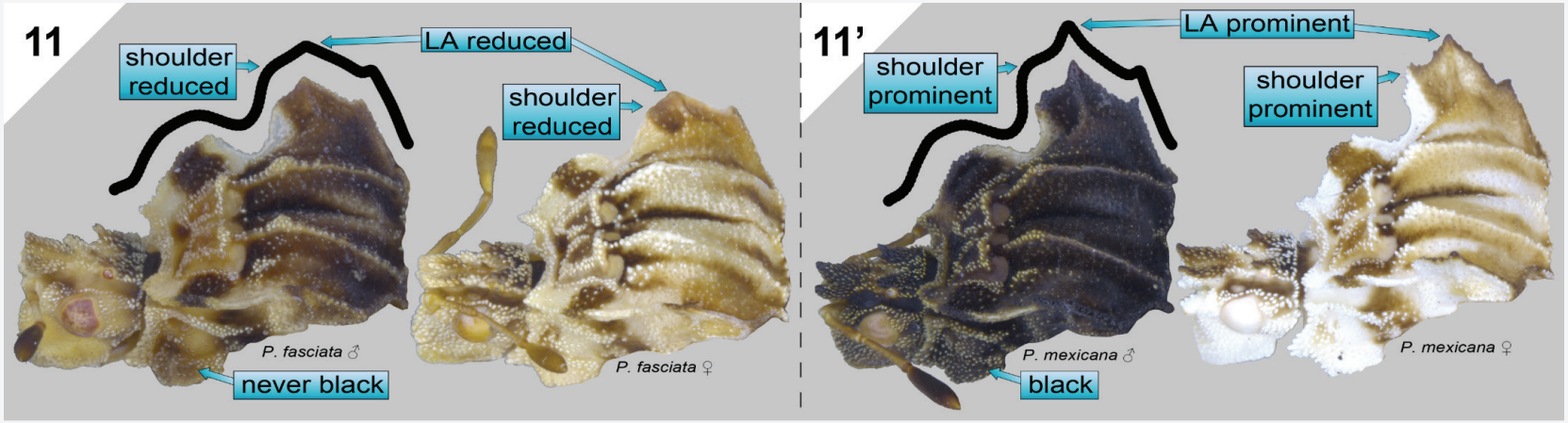
8) Lateral notch deep, the anterior pronotal lobe appearing very rounded and semicircular; prominent patch of granulation mesad to lateral notch present or absent; large, granulated protuberances of the pronotal carinae always present and prominent, often rising to a peak; connexivum of abdominal segment 4 concave and 5 convex, forming a sinuous margin.	8') Lateral notch of medium depth, giving the anterior pronotal lobe a flatter appearance; patch of granulation mesad to lateral notch usually absent, only sparsely granulated if present; protuberances of the pronotal carinae, reduced and low in most species; connexiva of abdominal segments 4 and 5 usually convex or straight.
9	12



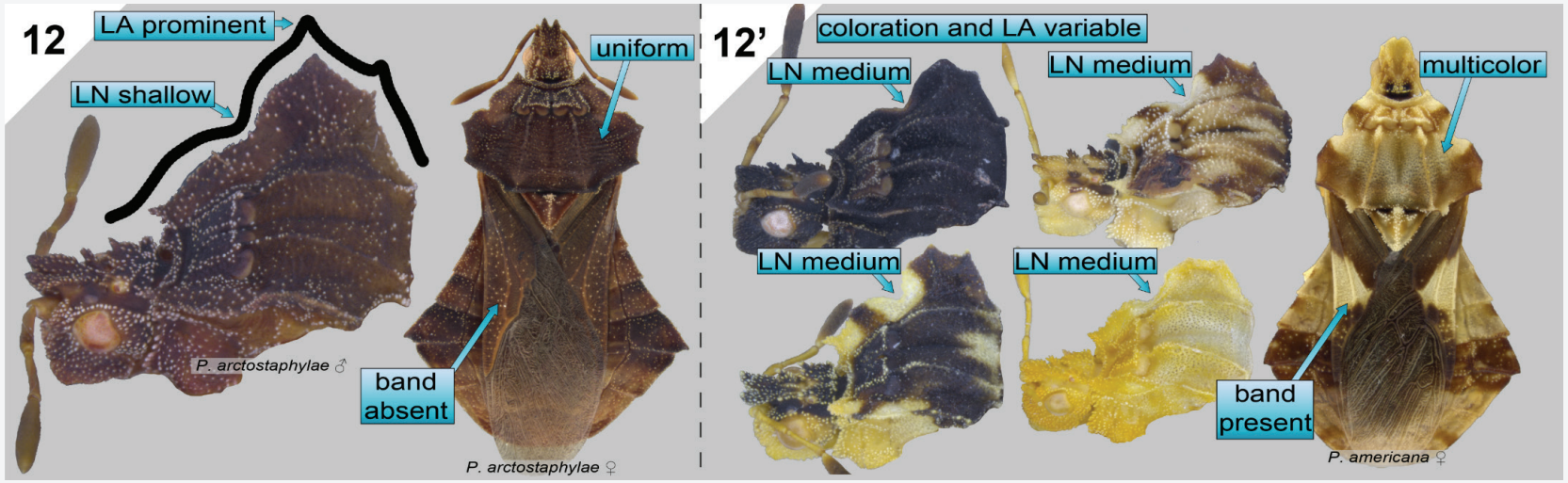
9) Medium size (♀ <~8.0 mm, ♂ <~7.5 mm); posterior lateral corners of connexiva of abdominal segments 2–5 weakly dentiform; abdomen barely dilated; connexivum of abdominal segment 6 rhomboidal; lateral notch deep; lateral angle slightly directed posteriad; posterior angle less prominent; restricted to California and Baja California.	9') Large size (♀ >~8.0 mm, ♂ >~7.5 mm); posterior lateral corners of connexiva of abdominal segments 2–5 strongly dentiform; abdomen broadly dilated; connexivum of abdominal segment 6 usually trapezoidal (sometimes rhomboidal in some *P. fasciata*); lateral notch very deep; lateral angle usually slightly directed anteriad; posterior angle either very prominent or distantly spaced from the lateral angle; distribution variable.
Phymata pacifica Evans, 1931	10



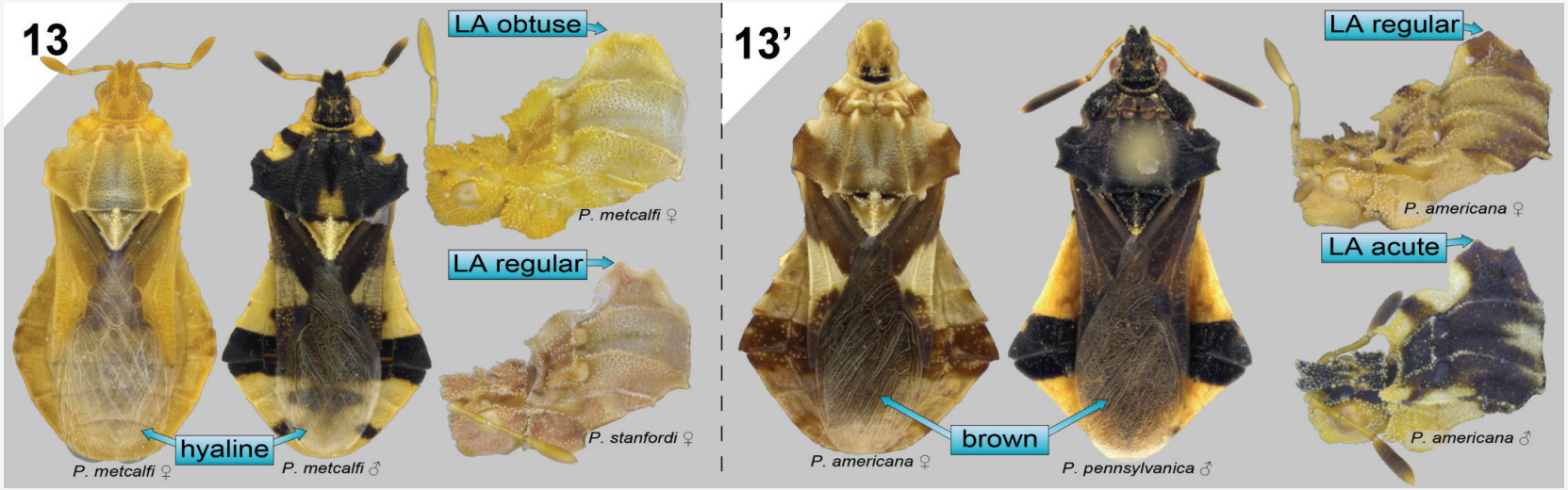
10) Posterior angle very prominent and acute, forming <135° angle with apices of lateral angle and posterior process; margin of anterior lobe never keeled; patch of granulation mesad to lateral notch absent; forefemur of males pale; restricted to the southeastern US.	10') Posterior angle reduced, forming >135° angle with apices of lateral angle and posterior process; margin of anterior lobe keeled; patch of granulation mesad to lateral notch always present; forefemur of males darkened (may be pale in teneral forms); distribution variable.
Phymata mystica Evans, 1931 stat. restit.	11



11) Lateral angle reduced, projecting dorsad and laterad; posterior lobe lacking prominent shoulder anterior to lateral angle; males never with black head and thorax; distributed across much of the central and eastern US (south of ~40°N) and into northern Mexico.	11') Lateral angle prominent, projecting dorsad and anteriad; posterior lobe with prominent shoulder anterior to lateral angle; males often with black head and thorax; restricted to Mexico and Central America.
Phymata fasciata (Gray, 1832)	*Phymata mexicana* Melin, 1931 stat. nov.



12) Body overall mahogany in color; corium unicolorous, without a conspicuous transverse marking; lateral notch relatively shallow; lateral angle very prominent; endemic to California and northern Baja California.	12') Body coloration variable, never mahogany; corium multicolored, with a conspicuous transverse marking lateral notch of medium depth; lateral angle variable; distribution variable.
Phymata arctostaphylae Van Duzee, 1914	13

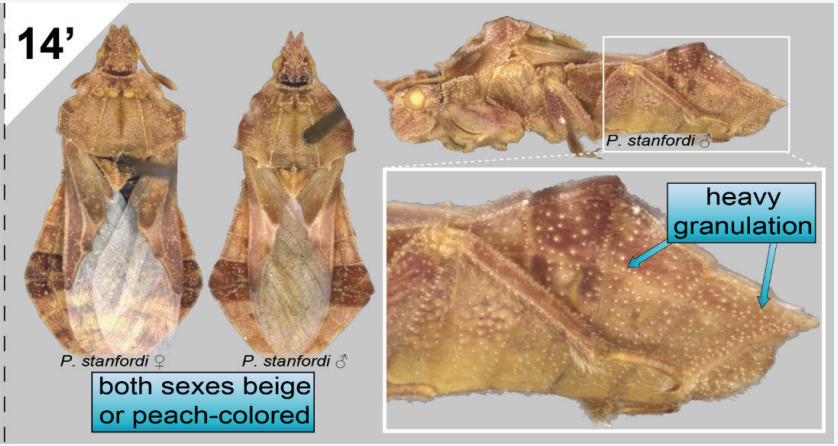


13) Wing membrane usually hyaline; size variable; lateral angles sometimes reduced and obtuse; found along Pacific Coast (Canada: British Columbia, US: California, Nevada, Oregon, Washington).

14

13') Wing membrane brownish; large (♀ >~8.0 mm, ♂ > ~7.5 mm); lateral angles always prominent, regular or acute; found across eastern North America and along the Rocky Mountains.

15

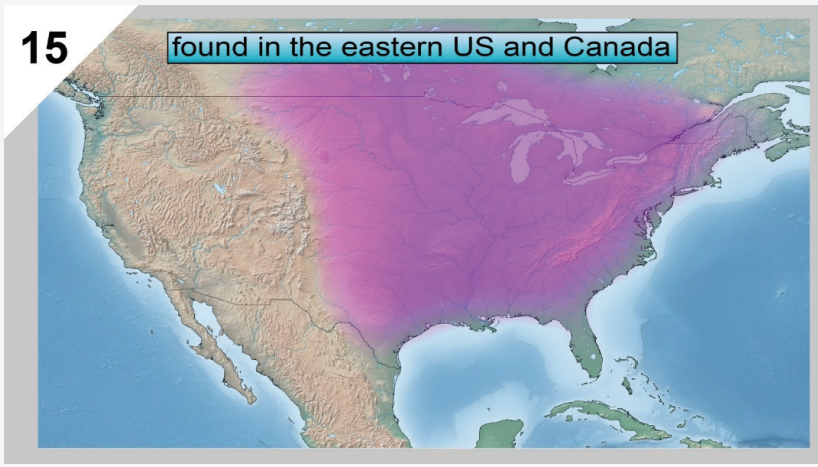


14) Body without extensive granulation; females usually predominantly yellow and/or light green, males usually yellow with brown or black markings; distributed from southern British Columbia to southern California.

Phymata metcalfi Evans, 1931 stat. restit.

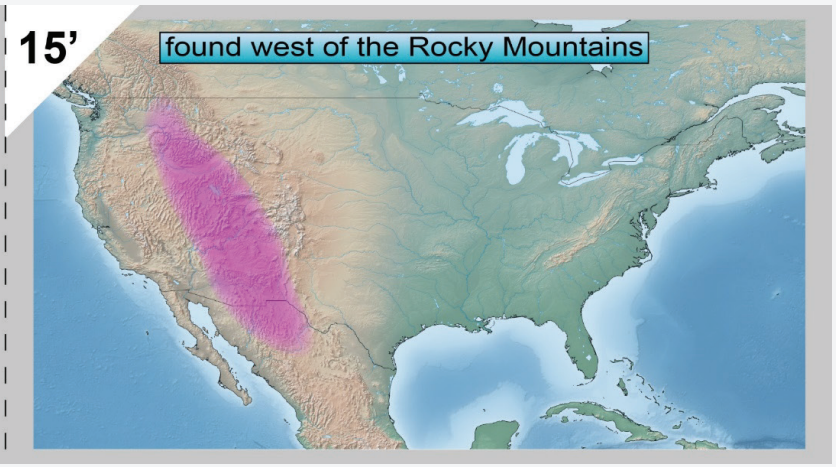
14') Extensive granulation across body; usually pinkish or beige overall, males with brown markings; restricted to the coastal ranges of northern and central California.

Phymata stanfordi Evans, 1931 stat. nov.



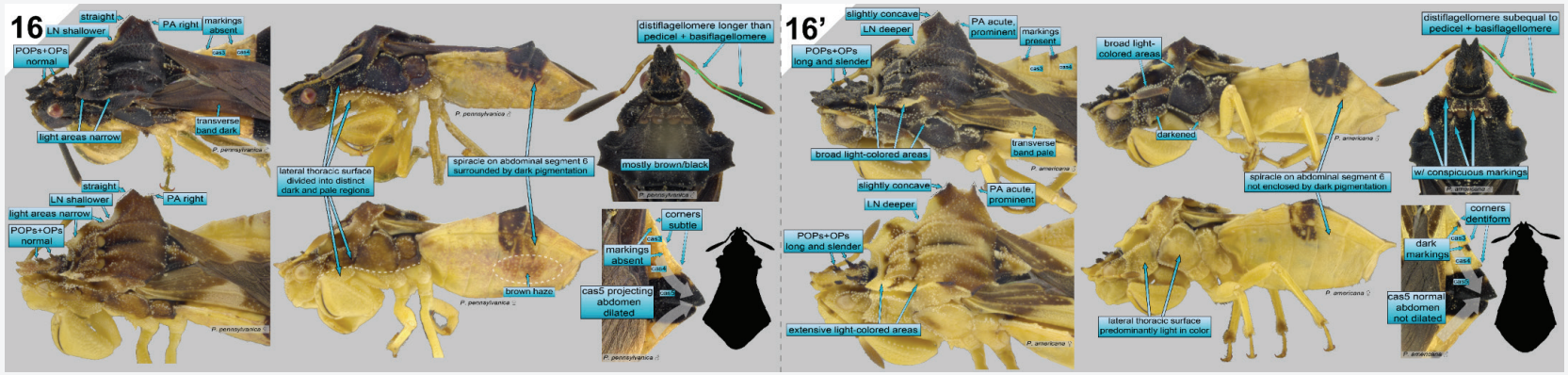
15) Found in the eastern US and Canada.

16



15') Found west of the Rocky Mountains.

17

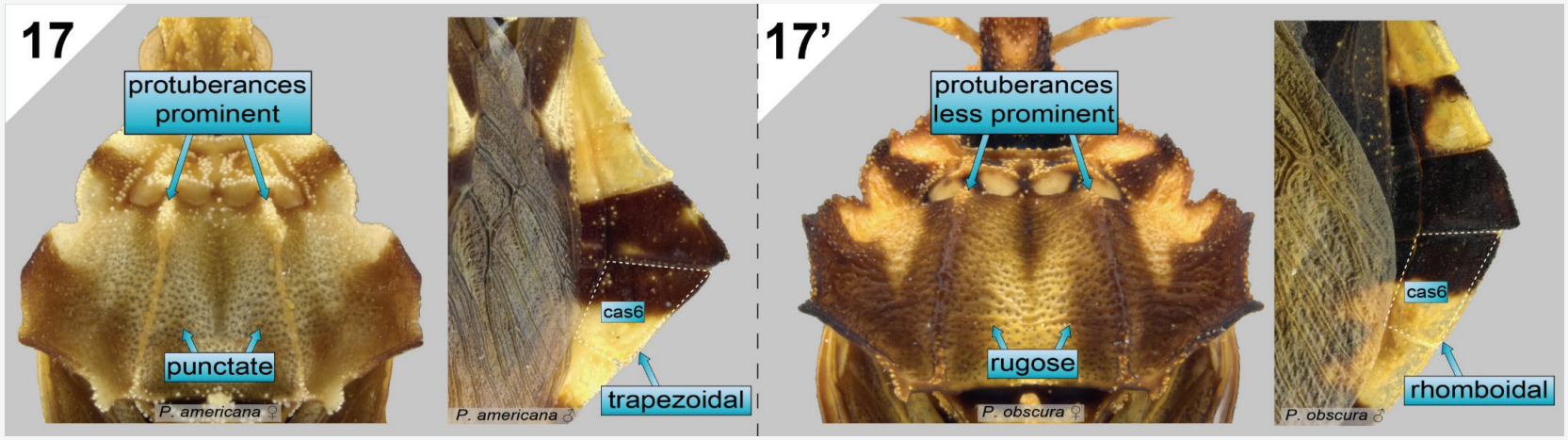


16) Distiflagellomere of males longer than pedicle + basiflagellomere; distiflagellomere of females only slightly shorter than pedicle + basiflagellomere; posterior lateral corners of connexiva of abdominal segments 2–4 smooth or subtle, anterior corners of connexiva of abdominal segments 3 and 4 usually without dark marking (northern populations might have these); pronotum relatively uniform in color being black in males and brown in females.

Phymata pennsylvanica Handlirsch, 1897

16') Distiflagellomere of males shorter than or subequal to pedicle + basiflagellomere; distiflagellomere of females considerably shorter than pedicle + basiflagellomere; posterior lateral corners of connexiva of abdominal segments 2–4 dentiform; anterior corners of connexiva of abdominal segments 3 and 4 usually with dark marking; pronotum color variable, often with light colored markings on anterior angle and around lateral notch.

Phymata americana Melin, 1931 [in part]



17) Usually with very prominent protuberances on longitudinal carina of pronotal hind disc; posterior pronotal disk between longitudinal carinae with punctate sculpturing; connexivum of abdominal segment 6 of males often trapezoidal with anterior margin conspicuously longer than posterior margin; broadly distributed across the southwestern US, and northern Mexico.

Phymata americana Melin, 1931 [in part]

17') Protuberances on longitudinal carina of pronotal hind disk less prominent; posterior pronotal disk between longitudinal carinae with rugose sculpturing; connexivum of abdominal segment 6 of males often rhomboidal with anterior and posterior margins of equal length; restricted to the northern Great Basin and Palouse region.

Phymata obscura Kormilev, 1957 stat. nov.

Nearctic *erosa* species group

Figs 3–22, Maps 1–17

Description: Medium to large-sized ambush bugs, total length: males ~6.0–9.5 mm, females ~6.5–11.0 mm; width across lateral angles of pronotum: ~2.2–3.8 mm. STRUCTURE: THORAX: pronotal margin between the lateral and posterior angles without a tooth-like process; scutellum cruciform or subcruciform; forewing membrane simple with two to three basal cells and multiple parallel veins, distal portion of wing membrane never with many anastomosed veins. ABDOMEN: broadened across the fifth abdominal segment, connexivum of abdominal segment 5 often expanded laterally but never bilobed (i.e., forming ultraconnexivum). COLORATION: variable.

Discussion: The vast majority of ambush bugs found in North America belong to the Nearctic *erosa* species group. These taxa can be distinguished from rarer fauna by their relatively large size, simple wing venation, and various pronotal, scutellar, and connexival characteristics described above and illustrated in the key.

***Phymata americana* Melin, 1931**

Figs 3A–F, 20A, 21A–D. Map 1.

Phymata americana Melin, 1931
Melin, 1931: p6 (original description); Kormilev, 1953: p66 (taxonomy); Kormilev, 1962: p412 (revision); Henry and Froeschner, 1988: p601 (catalog); Froeschner and Kormilev, 1989: p44 (catalog)

Phymata americana wisconsina Melin, 1931
Melin, 1931: p6 (original description)

Phymata americana coloradensis Melin, 1931 syn. nov.
Melin, 1931: p7 (original description); Henry and Froeschner, 1988: p603 (catalog); Froeschner and Kormilev, 1989: p45 (catalog)

Phymata americana ottawensis Melin, 1931
Melin, 1931: p7 (original description)

Phymata pennsylvanica americana Melin, 1931
Evans, 1931: p715 (revision)

Phymata americana americana Melin, 1931
Kormilev, 1953: p66 (taxonomy); Kormilev, 1962: p412 (revision); Henry and Froeschner, 1988: p601 (catalog); Froeschner and Kormilev, 1989: p44 (catalog)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) the relatively large size (~8–11 mm), (2) integument lacking elongated setaceous granulation, (3) lateral margin of anterior pronotal lobe never keeled, (4) lateral and posterior pronotal angles prominent and often acute, (5) posterior pronotal disk punctate, (6) connexiva of abdominal segments 3–4 pale, each usually with a dark marginal spot (may be absent in teneral forms), (7) lateral margins of connexiva of abdominal segments 4–5 more or less straight, and (8) wing membrane brownish.

Redescription: Male: Medium to large, total length: ~8.15–9.15 mm; width across lateral angles of pronotum: ~3.08–3.67 mm. STRUCTURE: HEAD (Fig. 3B): distiflagellomere shorter in length than pedicel + basiflagellomere (dflg : pd + bflg = ~0.89). THORAX (Fig. 3E, 20A): thoracic surface matte; anterior pronotal disk without elongated setaceous granulation; posterior pronotal disk punctate; area between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe either with diffuse granulation (most eastern populations) or without granulation (most western populations); longitudinal carina with or without prominent knoblike tubercle; lateral margin of anterior pronotal lobe not keeled; lateral notch of medium depth; lateral margin of pronotum from lateral notch to lateral angle smooth or with light crenulation; lateral angle prominent and acute; posterior angle prominent and acute; lateral surface of forefemur smooth or sparsely granulated; lateral surface of thorax smooth or sparsely granulated; forewing membrane brown, cloudy, not hyaline. ABDOMEN (Fig. 3C): posterior corners of connexiva of abdominal segments 2–4 weakly serrate or dentiform; lateral margins of connexiva of abdominal segments 4–5 more or less straight; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 less than twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 rhomboidal, anterior and posterior margin roughly the same width. COLORATION (Figs 3A-E): variable; anterior pronotal lobe usually with dark marking; forefemur pale, never darkened; corium with a conspicuous transverse band; lateral thoracic surface predominantly black, with light-colored granulation; connexiva of abdominal segments 3–4 usually with dark basal spots; spiracle of abdominal segment 6 usually not enclosed by dark pigmentation. Female: Large, total length: ~9.59–10.73 mm, width across lateral angles of pronotum: ~3.38–4.31 mm. COLORATION (Figs 3A,F): variable; generally much lighter in color overall than males; pronotum with large light-colored areas interspersed with brown markings; lateral thoracic surface predominantly light in color; lateroventral surface of abdominal sternites 5–7 without brownish coloration.

Biology: *Phymata americana* is typically found in open grasslands and shrublands and has been collected from a wide variety of flowering plants, particularly many species of Asteraceae. The presence of *P. americana* on flowering vegetation has been shown to affect the behavior of pollinators and other floral visitors (Elliott and Elliott 1991). The life history and broad predatory habits of *P. americana* were documented by Balduf (1939, 1940, 1941, 1943). Differences in feeding behavior and morphology of males and females were documented by

Mason (1977). Ambush site selection (patch choice) of *P. americana* has also been examined (Greco and Kevan 1995; Kevan and Greco 2001).

Distribution: Widespread, ranging across southern Canada, northeastern US, Great Lakes region, Great Plains, westward to the Rocky Mountains, and into the deserts and shrublands of the southwestern US and northern Mexico. While this species is found primarily east of the Rocky Mountains, specimens have been found as far west as Arizona. Based on our survey of museum material and iNaturalist observations, *P. americana* appears to be largely absent from the southeastern United States. Most *erosa* group specimens examined from this region fit the revised descriptions of other taxa (i.e., either *P. pennsylvanica*, *P. fasciata*, or *P. mystica*) more closely than the description of *P. americana* above.

Discussion: *Phymata americana* is one of the most common ambush bug species in North America and its broad geographic range has presumably resulted in morphological variation. Froeschner and Kormilev (1989) recognized four subspecies of *P. americana*. Molecular analyses have subsequently revealed that *P. americana* sensu lato consists of three distinct groupings, one that includes the nominate subspecies, *P. americana coloradensis*, and *P. pennsylvanica*, a second that consists of *P. americana metcalfi* and *P. pacifica stanfordi*, and a third represented by *P. americana obscura*, a species restricted to the northern Great Basin and Palouse region. *Phymata arctostaphylae* also renders *P. americana* sensu lato paraphyletic with it being more closely related to western *P. americana* subspecies (*metcalfi* and *obscura*) than eastern taxa. Given their divergent morphologies and distinct geographic ranges, we treat each of these groupings as a separate species and hereby synonymize *P. americana coloradensis* with the nominate subspecies. The main differences between these geographical varieties is coloration and the presence or absence of a prominent knoblike tubercle on each of the longitudinal carinae of the posterior pronotal lobe with the former (western populations) exhibiting lighter coloration and larger protuberances than the latter. Despite that molecular data sequenced to date have yet to clearly separate *P. americana* and *P. pennsylvanica* (see Masonick and Weirauch, 2020), we treat them as different species due to size and morphological differences (refer to Fig. 23). Punzalan and Rowe (2017) suggested that these two taxa likely engage in hybridization where they come into contact and may give rise to individuals that exhibit intermediate forms of the two phenotypes.

Identification remarks: *Phymata americana* typically lacks a very dense granulation patch (like that of *P. fasciata* or *P. pacifica*) between the lateral notch and longitudinal carina of the posterior pronotal lobe. Granulation is usually present and diffuse here on many specimens from the eastern United States and Canada (see pronotum of male and female specimens in Figs 3E–F). Specimens from western populations tend to lack granulation in this area. Some male specimens (particularly those from western North America) have serrate or dentiform connexiva on abdominal segments 2–4 and may exhibit relatively dilated abdomens that resemble *P. mystica* (see male *P. americana* specimen in Key(2) Couplet 17). The following characteristics of *P. americana* help to separate it from *P. pennsylvanica*: (1) males with a distiflagellomere that is shorter than the pedicel and flagellomere combined, never distinctly longer, (2) pronotum usually with large, conspicuous light colored markings (dark pigmentation of pronotum of *P. pennsylvanica* is typically more uniform and widespread), (3) transverse band on corium light in color, (4) uneven margins of connexiva of abdominal segments 2–4, (5) connexivum of abdominal segment 5 not abruptly dilated in males, (6) dark colored ventral region of pro- and mesopleura in males, (7) lack of dark pigmentation encircling spiracle on sternite 6, (8) presence of peaks or protuberances along the longitudinal carinae of the posterior pronotal lobe (these are especially prominent among western populations, see Key(2) Couplets 8' and 17 for examples of *P. americana* specimens with prominent peaks), and (9) presence of long and prominent multibranched preocellar and ocellar processes (these processes tend to be slightly smaller in *P. pennsylvanica*).

Type information: Melin's type series of *P. americana*, *P. americana coloradensis*, *P. americana ottawensis*, and *P. americana wisconsina* are deposited in the Swedish Museum of Natural History, Stockholm, Sweden. We here designate one of these specimens to serve as a lectotype for *P. americana*. As only images of a few specimens from these type series were examined for this study, we were unable to verify if the remaining syntypes are actually conspecific. Images of the following specimens were examined:

LECTOTYPE: (*Phymata americana* Melin, 1931): Male: **[country not specified]: Ottawa**, Johansen, (UCR_ENT 00123195) (NHRS-GULI000075674 (NRM). Fig. 21A. Image: http://www2.nrm.se/en/het_nrm/a/phymata_americana.html

SYNTYPE: (*Phymata americana coloradensis* Melin, 1931): Male: **USA: Colorado**, Morrison, (NRM). Fig. 21B. Image: http://www2.nrm.se/en/het_nrm/a/phymata_americanacoloradensis.html

SYNTYPE: (*Phymata americana ottawensis* Melin, 1931): Female: **[country not specified]: Ottawa**, Johansen, (NRM). Fig. 21C. Image: http://www2.nrm.se/en/het_nrm/a/phymata_americanaottawensis.html

SYNTYPE: (*Phymata americana wisconsina* Melin, 1931): Female: **USA: Wisconsin**, Kumlien, (NRM). Fig. 21D. Image: http://www2.nrm.se/en/het_nrm/a/phymata_americanawisconsina.html

Additional material examined: See Appendix; 1,265 specimens, including 755 adult males and 503 adult females.

Phymata arctostaphylae Van Duzee, 1914

Figs 4A–E, 20B, 21R. Map 2.

Phymata erosa arctostaphylae Van Duzee, 1914
Van Duzee, 1914: p11 (original description)

Phymata arctostaphylae Van Duzee, 1914
Evans, 1931: p719 (revision); Kormilev, 1962: p404 (revision); Henry and Froeschner, 1988: p602 (catalog); Froeschner and Kormilev, 1989: p45 (catalog)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) the relatively large size (~7.5–10 mm), (2) dark red to mahogany body color, and (3) corium without a conspicuous transverse band.

Redescription: Male: Medium to large, total length: ~7.70–8.61 mm, width across lateral angles of pronotum: ~3.06–3.65 mm. STRUCTURE: HEAD (Fig. 4A): distiflagellomere subequal to or longer than pedicel + basiflagellomere (dflg : pd + bflg = ~1.04). THORAX (Figs 4A,D, 20B): thoracic surface matte; anterior pronotal disk without elongated setaceous granulation; posterior pronotal disk rugose; area between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe usually devoid of granulation; longitudinal carina without prominent tubercle; lateral margin of anterior pronotal lobe not keeled; lateral notch of medium depth; lateral margin of pronotum from lateral notch to lateral angle smooth or with light crenulation; lateral angle prominent and acute; posterior angle prominent and acute; lateral surface of forefemur smooth or sparsely granulated; lateral surface of thorax smooth or sparsely granulated; forewing membrane hyaline. ABDOMEN (Fig. 4B): posterior corners of connexiva of abdominal segments 2–4 weakly serrate or dentiform; lateral margins of connexiva of abdominal segments 4–5 sinuous; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 trapezoidal, anterior margin roughly twice as wide as posterior margin. COLORATION (Figs 4A): body predominantly dark red to mahogany in color, head and thorax sometimes very dark, usually with lightly colored fine granulation; anterior pronotal lobe never with contrasting marking; forefemur dark red; corium without a conspicuous transverse band. Female: Large, total length: ~8.96–10.14 mm, width across lateral angles of pronotum: ~3.43–4.09 mm. STRUCTURE: HEAD (Fig. 4A): distiflagellomere shorter than length to pedicel + basiflagellomere (dflg : pd + bflg = ~0.78). COLORATION (Fig. 4A): mostly dark red to mahogany, similar to males but slightly less dark overall.

Biology: *Phymata arctostaphylae* inhabits chaparral of California and northern Baja California's coastal mountain ranges and has been collected from *Arctostaphylos* Adans. spp. manazanitas (Ericaceae) during the months of August through October. Despite its frequently noted association with *Arctostaphylos*, both males and females have also been collected from various Asteraceae including *Haplopappus* Cass., *Chrysanthemum* L., and *Gutierrezia* Lag. Specimens have been collected at elevations ranging between 22–2,014 m above sea level.

Distribution: Endemic to south/central California and northern Baja California.

Discussion: This striking species is rarely encountered in the wild and represented by relatively few specimens in entomological collections. Based on molecular data, *P. arctostaphylae* appears to be very closely related to other western members of the *americana* species complex (i.e., *P. metcalfi* and *P. obscura*) (Masonick and Weirauch, 2020).

Identification remarks: Along with male *P. pennsylvanica*, male *P. arctostaphylae* are the only members of the *erosa* group with distiflagellomeres that exceed the combined lengths of the preceding two segments. Other than this and its distinctive coloration, useful characteristics that help distinguish *P. arctostaphylae* from other Nearctic *erosa* group taxa include: (1) hyaline forewing membranes, (2) shallow lateral notch (relative to other members of the *americana* species complex), (3) dorsal surface of pronotum uniform in color with fine, lightly colored granulation, and (4) absence of granulation patch on the pronotum between lateral notch and longitudinal carina.

Type information: The holotype is located at the California Academy of Sciences and is a female specimen beaten from *Arctostaphylos* near Morena Dam in southern California (Van Duzee 1914). Only images of this specimen were examined.

HOLOTYPE: Female: **USA: California: *San Diego Co.:*** 15 Oct 1913, E. P. Van Duzee (CAS). Fig. 21R

Additional material examined: See Appendix; 55 specimens, including 23 adult males and 31 adult females.

Phymata borica Evans, 1931

Figs 5A–E, 20C. Map 3.

Phymata borica Evans, 1931
Evans, 1931: p721 (original description); Kormilev, 1962: p416 (revision); Henry and Froeschner, 1988: p602 (catalog); Froeschner and Kormilev, 1989: p46 (catalog)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) a very shallow lateral notch of the pronotum, (2) a posterior pronotal angle that is obtuse and weakly developed, (3) a relatively short and blunt frontal process, and (4) pinkish body color (especially in females).

Redescription: Male: Small to medium, total length ~6.93–7.69 mm, width across lateral angles of pronotum: ~2.56–2.65 mm. STRUCTURE: HEAD (Fig. 5): distiflagellomere of male shorter than pedicel + basiflagellomere. THORAX (Figs 5A,D, 20C): thoracic surface matte; anterior pronotal disk without elongated setaceous granulation; posterior pronotal disk punctate; area between lateral pronotal notch and longitudinal carina of the posterior pronotal either with diffuse granulation or devoid of granulation; longitudinal carina without prominent tubercle; lateral margin of anterior pronotal lobe not keeled and inconspicuous; lateral notch shallow; lateral margin of pronotum from lateral notch to lateral angle smooth or with light crenulation; lateral angle small and obtuse; posterior angle small and obtuse; lateral surface of forefemur smooth or sparsely granulated; lateral surface of thorax smooth or sparsely granulated; forewing membrane brown, cloudy, never hyaline. ABDOMEN (Fig. 5B): posterior corners of connexiva of abdominal segment 2–4 inconspicuous/subtle; lateral margins of connexiva of abdominal segments 4–5 convex; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 less than twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 rhomboidal, anterior and posterior margin roughly the same width. COLORATION (Figs 5A,B,D): variable; anterior pronotal lobe usually with dark marking; forefemur sometimes darkened; corium with a conspicuous transverse band; sometimes pinkish or yellowish with brown and/or black markings; live specimens may even appear greenish. Female: Medium, total length: ~8.19–8.62 mm, width across lateral angles of pronotum: ~2.89–3.07 mm. COLORATION (Figs 5A,B,C,E): usually pinkish or pinkish-brown with brown markings.

Biology: *P. borica* has been collected from *Solidago* L. (Asteraceae), *Mimosa* L. (Fabaceae), and *Sphaeralcea* A. St.-Hil. (Malvaceae). Adults are found primarily from June through September. Specimens have been collected at elevations ranging between 1,219–2,316 m above sea level.

Distribution: This species is native to the Colorado Plateau region of the United States and is found across Arizona, southwestern Colorado, New Mexico, and southern Utah.

Discussion: *Phymata borica* morphologically resembles two other species that are found elsewhere in the southwestern United States, *P. luteomarginata* and *P. paraborica* sp. nov., and is closely related to *P. rossi*, a species with which it is sympatric (Masonick and Weirauch, 2020).

Identification remarks: When viewed dorsally, the abdominal outline of females may appear relatively round (see Figs 5A,C). In contrast to *P. luteomarginata*, *P. borica* either lacks or only has diffuse granulation between the lateral pronotal notch and longitudinal carina of the posterior pronotal lobe and always has brownish forewing membranes. *Phymata borica* males sometimes have darkened forelegs, a trait that is never exhibited by *P. luteomarginata* or *P. paraborica* sp. nov. males.

Type information: Only a paratype of this species from the Biodiversity Institute & Natural History Museum at the University of Kansas was examined. The holotype is housed in the same collection.

HOLOTYPE: *Phymata borica*, 1931: Male: **USA: Utah:** Zion National Park, 13 Jul 1929, R. H. Beamer, (KU).

PARATYPE: **USA: Arizona:** S. Arizona, 32.74976°N, 111.66501°W, Aug 1902, F. H. Snow, 1♂ (UCR_ENT 00070065) (KU).

Additional material examined: See Appendix; 41 specimens, including 18 adult males and 23 adult females.

Phymata fasciata (Gray, 1832)

Figs 6A–E, 20D, 21F. Map 4.

Syrtis fasciatus Gray, 1832
Gray, 1832: p242 (original description)

Phymata wolffi Stål, 1876
Stål, 1876: p133 (original description); Kormilev, 1962: p406 (synonymy)

Phymata fasciata (Gray, 1832)
Melin, 1931: p9 (revision); Kormilev, 1962: p305 (revision); Henry and Froeschner, 1988: p602 (catalog); Froeschner and Kormilev, 1989: p51 (catalog)

Phymata fasciata georgiensis Melin, 1931
Melin, 1931: p9 (original description); Kormilev, 1962: p406 (synonymy)

Phymata fasciata fasciata (Gray, 1832)
Kormilev, 1962: p305 (revision); Henry and Froeschner, 1988: p603 (catalog); Froeschner and Kormilev, 1989: p52 (catalog)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) large size (females > ~8 mm, males > ~7.5 mm), (2) deep lateral notch, (3) integument lacking elongated setaceous granulation, (4) keeled margin of the anterior pronotal lobe, (5) conspicuous cluster of raised granules on the pronotum mesad to lateral notch, and (6) a right or obtuse lateral angle.

Redescription: Male: Medium to large, total length: ~7.61–9.07 mm, width across lateral angles of pronotum: ~2.97–3.40 mm. STRUCTURE: HEAD (Fig. 6A): distiflagellomere of male shorter than pedicel + basiflagellomere. THORAX (Figs 6A,D, 20D): thoracic surface glossy; anterior pronotal disk without elongated setaceous granulation; posterior pronotal disk punctate; area between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe with a distinct granulation patch; longitudinal carina with prominent

knoblike tubercle; lateral margin of anterior pronotal lobe keeled and semicircular; lateral notch deep; lateral margin of pronotum from lateral notch to lateral angle smooth or with light crenulation; lateral angle right or obtuse; posterior angle prominent, right or acute; lateral surface of forefemur smooth or sparsely granulated; lateral surface of thorax moderately granulated; forewing membrane brown, cloudy, never hyaline. ABDOMEN (Fig. 6B): posterior corners of connexiva of abdominal segments 2–4 strongly serrate or dentiform; lateral margins of connexiva of abdominal segments 4–5 sinuous; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 less than twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 rhomboidal, anterior and posterior margin roughly the same width. COLORATION (Figs 6A–D): variable; body usually sepia or cream colored and marked with brown bands; thorax, corium, and connexiva with soft pink or roseate colored markings; anterior pronotal lobe usually with a well-defined light-colored "M"-shaped pattern that is bordered by strong dark markings; forefemur darkened (olive green, brown, or blackish); corium with a conspicuous transverse band. Female: Medium to large, total length: ~8.62–9.60 mm, width across lateral angles of pronotum: ~3.25–3.73 mm. THORAX (Fig. 6E): lateral angle obtuse. COLORATION (Figs 6A,B,E): variable; generally similar to that of males but overall lighter in color and the forefemur pale, never darkened.

Biology: *Phymata fasciata* has been collected from a broad range of flowering plants spanning at least ten different families and a number of host plants unique for *erosa* group taxa including *Cacalia* Kuntze, *Conoclinium* DC., *Helenium* L., *Leucanthemum* Mill., *Sedum* L., *Geranium* L., *Mentha* L., *Pycnanthemum* Michx., *Clematis* L., *Cephalanthus* L., and *Verbena* L.. Dodson and Marshall (1984) documented postcopulatory mate guarding behavior in *P. fasciata* and demonstrated evidence that sexual selection may favor males with longer hind legs. Specimens have been collected at elevations ranging between 2–1,963 m above sea level.

Distribution: This widespread species is found throughout the southeastern United States, New England, southern Great Plains and as far west as Arizona and south into Mexico. The northern limit of the range of *P. fasciata* corresponds roughly to the 40th parallel north. This species is mostly absent from the Great Lakes region and likely does not occur in Canada. Based on our survey of museum specimens, iNaturalist observations, and new state records reported by Swanson et al. (2017) and Swanson (2019), it is clear that the range of this species extends far into the interior of North America and is not confined along the Atlantic and Gulf Coasts.

Discussion: *Phymata fasciata* is one of the most common species of ambush bugs in eastern North America. The *P. fasciata* treated by Kormilev (1962) included three subspecies in addition to the nominate. Two of these subspecies, *P. fasciata mexicana* and *P. fasciata mystica* are elevated here to species rank based on differences in their morphology and molecular evidence (see Masonick and Weirauch, 2020). The remaining subspecies, *Phymata fasciata panamensis* Kormilev, 1962 from Panama, is herein synonymized with *P. mexicana*. *Phymata fasciata* overlaps with many species across its broad range but can be distinguished using the morphological characters highlighted above.

Identification remarks: In addition to the characters highlighted in the diagnosis, *P. fasciata* can be recognized by (1) the semicircular outline of the anterior pronotal lobe, (2) prominent knoblike tubercle on the longitudinal pronotal carina, (3) sinuous lateral margin of connexiva of abdominal segments 4–5, (4) glossy thoracic cuticle, and (5) well-defined "M"-shaped banding pattern on the posterior lobe. This species shares much in common with *P. mexicana* but has a more subtle lateral angle, a posterior corner of the connexivum of abdominal segment 5 that is less sharp/acute, and lighter coloration. Males often have darkened heads, thoracic segments, and forelegs, but these areas are never quite as dark as that of *P. mexicana*.

Type information: Kormilev (1962) designated the type of *Phymata fasciata georgiensis* Melin as the neotype for *Phymata fasciata* (Gray) and deposited it in the Swedish Museum of Natural History, Stockholm, Sweden. Only images of this type were examined.

NEOTYPE: Male: **USA: Georgia**, Morrison (NRM). Fig. 21F. Image: http://www2.nrm.se/en/het_nrm/f/phymata_fasciatageorgiensis.html

Additional material examined: See Appendix; 285 specimens, including 158 adult males and 124 adult females.

Phymata granulosa Handlirsch, 1897

Figs 7A–E, 20E, 21G+H+L. Map 5.

Phymata erosa granulosa Handlirsch, 1897
Handlirsch, 1897: p163 (original description)

Phymata granulosa Handlirsch, 1897
Melin, 1931: p15 (taxonomy); Henry and Froeschner, 1988: p603 (catalog); Froeschner and Kormilev, 1989: p52 (catalog)

Phymata granulosa granulosa Handlirsch, 1897
Kormilev, 1962: p396 (revision); Froeschner and Kormilev, 1989: p53 (catalog)

Phymata chiriquiensis Melin, 1931
Melin, 1931: p18 (taxonomy)

Phymata granulosa chiriquiensis Melin, 1931 syn. nov.
Kormilev, 1962: p398 (revision)

Phymata granulosa evansi Kormilev, 1962 syn. nov.
Kormilev, 1962: p399 (original description); Froeschner and Kormilev, 1989: p53 (catalog)

Diagnosis: Recognized from other species of the

Nearctic *erosa* group by the following combination of characters: (1) the relatively large size (~8–10 mm), (2) abundance of setaceous granulation on the anterior pronotal disc, lateral thoracic surface, and on forefemur, with heavy, low granulation scattered across other areas of the body, and (3) lateral margins of connexiva of abdominal segments 3–6 relatively smooth, not roughly crenulated.

Redescription: Male: Medium to large, total length: ~7.89–9.52 mm, width across lateral angles of pronotum: ~3.18–3.78 mm. STRUCTURE: HEAD (Fig. 7A): distiflagellomere of male shorter than pedicel + basiflagellomere. THORAX (Figs 7A,C,D, 20E): thoracic surface matte; anterior pronotal disk with elongated setaceous granulation; posterior pronotal disk punctate; area between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe with a distinct granulation patch; longitudinal carina with or without prominent tubercle; lateral margin of anterior pronotal lobe not keeled; lateral notch of medium depth; lateral margin of pronotum from lateral notch to lateral angle heavily crenulated with prominent tubercles; lateral angle prominent and acute; posterior angle prominent and acute; lateral surface of forefemur heavily granulated; lateral surface of thorax heavily granulated; forewing membrane brown, cloudy, never hyaline. ABDOMEN (Fig. 7B): posterior corners of connexiva of abdominal segments 2–4 strongly serrate or dentiform; lateral margins of connexiva of abdominal segments 4–5 sinuous; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 trapezoidal, anterior margin roughly twice as wide as posterior margin. COLORATION (Figs 7A–D): variable; anterior pronotal lobe usually with dark marking; forefemur darkened; corium with a conspicuous transverse band. Female: Large, total length: ~8.89–10.11 mm, width across lateral angles of pronotum: ~3.57–4.28 mm. COLORATION (Figs 7A,B,E): generally similar to that of males, but lighter overall; forefemur pale, never darkened.

Biology: *Phymata granulosa* has been collected from Fabaceae, and like many other ambush bug species, it is likely that its host range encompasses a broader spectrum than what has been recorded. Specimens have been collected at elevations ranging between 134–1,580 m above sea level.

Distribution: This species ranges across central and southern Mexico (including the Yucatan Peninsula) and deep into Central America as the holotype of *Phymata granulosa chiriquiensis* Melin, 1931 was collected in Panama.

Discussion: The subspecies *Phymata granulosa chiriquiensis* Melin, 1931 and *Phymata granulosa evansi* Kormilev, 1962 are here synonymized with *P. granulosa*. Kormilev (1957) described one subspecies (*P. granulosa texasana*) based on a singleton male from the Chisos Mountains of southern Texas. All other subspecies of *P. granulosa* were described from considerably further south in Mexico or elsewhere in Central America. Based on the holotype's pronotal shape (very acute, posteriorly directed lateral angle), light coloration of the lateral surface of the thorax and forelegs, and its relatively small size, this specimen shares more similarities with *P. rossi* than *P. granulosa* and is thus synonymized with the former.

Identification remarks: While *P. granulosa*, *P. rossi*, and *P. saileri* all possess an abundance of setaceous elongated granulation on their thorax and legs, *P. granulosa* can best be distinguished from these other taxa based on: (1) the more dorsally projected regular (right angled) lateral and posterior pronotal angles (as opposed to being more posteriorly projected and acute) and (2) relatively smooth lateral margin of the connexiva of abdominal segments 3–6, with that of segment 5 being more or less straight or slightly convex and not sinuous.

Type information: Kormilev (1962) designated a lectotype for *P. granulosa* that is deposited in the Swedish Museum of Natural History, Stockholm, Sweden. Only images of this type were examined. Images of a syntype of *P. granulosa chiriquiensis* were also examined. Kormilev's holotype of *P. granulosa evansi* was examined and is deposited in the United States National Museum of Natural History in Washington D.C.

LECTOTYPE: (*Phymata granulosa* Handlirsch, 1897): Male: **MEXICO**, Sallé, (NRM). Fig. 21G. Image: http://www2.nrm.se/en/het_nrm/g/phymata_granulosa.html

SYNTYPE: (*Phymata granulosa chiriquiensis* Melin, 1931): Male: **PANAMA:** Volcán Chiriquí, Champion

(NRM). Fig. 21H. Image: http://www2.nrm.se/en/het_nrm/c/phymata_chiriquiensis.html

HOLOTYPE: (*Phymata granulosa evansi* Kormilev, 1962): Male: **MEXICO: Oaxaca:** Almolaya, F. Knab, (UCR_ENT 00008096) (USNM). Fig. 21L.

Additional material examined: See Appendix; 43 specimens, including 27 adult males and 16 adult females.

Phymata luteomarginata Kormilev, 1957

Figs 8A–E, 20F, 21N. Map 6.

Phymata luteo-marginata [sic] Kormilev, 1957
Kormilev, 1957: p130 (original description)

Phymata luteomarginata Kormilev, 1957
Kormilev, 1962: p472 (revision); Henry and Froeschner, 1988: p603 (catalog); Froeschner and Kormilev, 1989: p54 (catalog)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) shallow lateral notch, (2) crenulated lateral pronotal margin, and (3) conspicuous right or acute posterior angle.

Redescription: Male: Small to medium, total length ~6.30–7.45 mm, width across lateral angles of pronotum: ~2.27–2.99 mm. STRUCTURE: HEAD (Fig. 8D): distiflagellomere of male subequal in length to pedicel + basiflagellomere. THORAX (Figs 8A,C,D, 20F): thoracic surface matte; anterior pronotal disk sometimes with very short setaceous granulation; posterior pronotal disk rugose in some populations; area between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe usually with diffuse granulation; longitudinal carina without prominent tubercle; lateral margin of anterior pronotal lobe not keeled and lightly crenulated; lateral notch shallow or of medium depth; lateral margin of pronotum from lateral notch to lateral angle smooth or with light crenulation; lateral angle right or acute; posterior angle prominent and acute; lateral surface of forefemur smooth or sparsely granulated; lateral surface of thorax smooth or sparsely granulated; forewing membrane hyaline or brown. ABDOMEN (Fig. 8B): posterior corners of connexiva of abdominal segments 2–4 inconspicuous/subtle; lateral margins of connexiva of abdominal segments 4–5 sinuous or convex; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 less than twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 rhomboidal, anterior and posterior margin roughly the same width. COLORATION (Figs 8A–D): variable; anterior pronotal lobe with or without dark marking; forefemur pale, never darkened; corium with a conspicuous transverse band; connexiva of abdominal segments 3–4 usually without dark basal spots. Female: Small to medium, total length: ~6.99–8.97 mm, width across lateral angles of pronotum: ~2.63–3.23 mm. COLORATION (Figs 8A,B,E): similar to male but generally lighter-colored overall, body usually pale-yellow with brown markings.

Biology: This species has been collected from *Eriogonum fasciculatum* Benth. (Polygonaceae), *Sphaeralcea* A. St.-Hil. (Malvaceae), and *Purshia* DC. ex Poir. (Rosaceae).

Distribution: Found primarily in the Mojave and Great Basin Deserts of California and Nevada. Populations also inhabit portions of the Sierra Nevada mountain range.

Discussion: Kormilev (1957) described *P. luteomarginata* from a singleton male specimen and designated no secondary types. He was particularly struck by this specimen's unusual coloration having a mostly pale-yellow anterior pronotal lobe and testaceous (reddish-brown) remainder of the pronotum. We here expand the concept of *P. luteomarginata* to include slightly darker forms found elsewhere in the Mojave and southern Great Basin Region. *Phymata luteomarginata* is morphologically similar to both *P. borica* and *P. paraborica* sp. nov. but can be distinguished using molecular data (Masonick and Weirauch, 2020) and the combination of characters given in the diagnosis and identification remarks below.

Identification remarks: The following attributes can help distinguish *P. luteomarginata* from other western taxa: (1) well-developed and diverging frontal processes (compare with *P. borica* or *P. paraborica)*, (2) flattened anterior pronotal disk with very small setaceous granulation and a pair of small raised tubercles along its posterior margin (compare with *P. metcalfi* or *P. paraborica* sp. nov.), (3) rugose posterior pronotal disk, and (4) distiflagellomere of males subequal to pedicle + basiflagellomere. The lateral notch of *P. luteomarginata* tends to be deeper than that of *P. borica* or *P. paraborica* sp. nov. Many *P. luteomarginata* specimens have short setaceous granulation covering parts of the head and thorax, however this granulation is never as elongate as in *P. rossi* or *P. saileri*. *Phymata luteomarginata* inhabiting the Sierra Nevada mountains have cloudier forewing membranes and darker coloration overall than those found elsewhere.

Type information: The holotype was examined and is deposited in the National Museum of Natural History in Washington D.C.

HOLOTYPE: Male: **USA: Nevada:** Dixie N. F., 01 Jul 1937, D. J. & J. N. Knull (UCR_ENT 00008099) (USNM). Fig. 21N.

Additional material examined: See Appendix; 38 specimens, including 25 adult males and 13 adult females.

Phymata metcalfi Evans, 1931 stat. restit.

Figs 9A–E, 20G, 21S. Map 7.

Phymata metcalfi Evans, 1931

Evans, 1931: p723 (original description)

Phymata americana metcalfi Evans, 1931

Kormilev, 1962: p414 (revision); Henry and Froeschner, 1988: p602 (catalog); Froeschner and Kormilev 1989: p45 (catalog)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) lateral notch of medium depth, (2) integument lacking elongated setaceous or extensive granulation, (3) absence of granulation patch between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe, (4) punctate posterior pronotal disk, (5) prominent lateral angle, usually right or obtuse, (6) prominent posterior angle, usually acute or right, and (7) forewing membrane usually hyaline.

Redescription: Male: Medium to large, total length: ~7.16–8.49 mm, width across lateral angles of pronotum: ~2.68–3.43 mm. STRUCTURE: HEAD (Fig. 9A,D): distiflagellomere of male shorter than pedicel + basiflagellomere. THORAX (Figs 9A,D, 20G): thoracic surface matte; anterior pronotal disk without elongated setaceous granulation; posterior pronotal disk punctate; area between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe usually devoid of granulation; longitudinal carina without prominent tubercle; lateral margin of anterior pronotal lobe not keeled; lateral notch of medium depth; lateral margin of pronotum from lateral notch to lateral angle smooth or with light crenulation; lateral angle prominent and acute; posterior angle prominent and acute; lateral surface of forefemur smooth or sparsely granulated; lateral surface of thorax smooth or sparsely granulated; forewing membrane usually hyaline, brown in some populations. ABDOMEN (Fig. 9B): posterior corners of connexiva of abdominal segments 2–4 weakly serrate or dentiform; lateral margins of connexiva of abdominal segments 4–5 sinuous; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 less than twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 rhomboidal, anterior and posterior margin roughly the same width. COLORATION (Figs 9A,B,D): variable; anterior pronotal lobe usually with dark marking; forefemur pale, never darkened; corium with a conspicuous transverse. Female: Size variable, total length: ~7.47–9.25 mm, width across lateral angles of pronotum: ~2.79–3.44 mm. COLORATION (Figs 9A,B,C,E): variable.

Biology: *Phymata metcalfi* has been found on a broad range of hosts including Apocynaceae, Asteraceae, Lamiaceae, Malvaceae, Polygonaceae, and Rosaceae.

Distribution: This species is distributed from southern California to British Columbia.

Discussion and identification remarks: Based on morphological and molecular differences between *P. metcalfi*, *P. americana*, and *P. obscura*, we here elevate this taxon back to its original rank of species. Both *P. metcalfi* and *P. stanfordi* are relatively smaller than other members of the *americana* species complex (~7–9 mm in length). *Phymata metcalfi* varies greatly in size and color across its distribution. Southern individuals (mainly of the Mojave Desert) are often smaller and appear mostly yellow and lack the dark pronotal and connexival markings that are common among northern individuals. The lateral pronotal angle of specimens from the southern Mojave is often more reduced and obtuse (especially in females) than those from northern populations. *Phymata metcalfi* is morphologically very similar to *P. obscura* and is best separated using molecular data and geography. Molecular evidence and pronotal geometric morphometrics has failed to separate *P. metcalfi* and *P. stanfordi*. Nevertheless, we treat the two as distinct species based on coloration, degree of granulation across the body, and their geographical distribution. While *P. metcalfi* is distributed across most of California, *P. stanfordi* is found primarily in the coastal mountain ranges west of the Central Valley.

Type information: The holotype is deposited in the California Academy of Sciences. Only images of this specimen were examined.

HOLOTYPE: Male: **USA: Oregon: *Lake Co.:*** Summer Lake, 28 Jul 1930, H. A. Scullen, (CAS). Fig. 21S

PARATYPES: **CANADA: British Columbia:** Lillooet, 50.68652°N, 121.93347°W, 02 Sep 1918, Unknown, 1♂ (UCR_ENT 00047811), 1♀ (UCR_ENT 00047812) (CAS).

Additional material examined: See Appendix; 684 specimens, including 396 adult males and 281 adult females.

Phymata mexicana Melin, 1931 stat. nov.

Figs 10A–E, 20H, 21I+K. Map 8.

Phymata fasciata mexicana Melin, 1931

Melin, 1931: p10 (original description); Froeschner and Kormilev, 1989: p52 (catalog, listed as *Phymata fasciata mexicanus* [sic]); Kormilev, 1962: p409 (revision)

Phymata fasciata panamensis Kormilev, 1962 syn. nov.

Kormilev, 1962: p411 (original description)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) the relatively large size (~8–10 mm), (2) deep lateral notch, (3) integument lacking elongated setaceous granulation, (4) keeled margin of the anterior pronotal lobe, (5) conspicuous cluster of raised granules on the pronotum mesad to lateral notch, and (6) a very prominent acute lateral angle.

Redescription: Male: Large, total length: ~8.14–9.80 mm, width across lateral angles of pronotum: ~3.29–4.06 mm. STRUCTURE: HEAD (Fig. 10A): distiflagellomere of male shorter than pedicel + basiflagellomere. THORAX (Figs 10A,C,D, 20H): thoracic surface glossy; anterior pronotal disk without elongated setaceous granulation; posterior pronotal disk punctate; area between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe with a distinct granulation patch; longitudinal carina with prominent knoblike tubercle; lateral margin of anterior pronotal lobe keeled and semicircular; lateral notch deep; lateral margin of pronotum from lateral notch to lateral angle smooth or with light crenulation; lateral angle prominent and acute; posterior angle prominent, right or acute; lateral surface of forefemur smooth or sparsely granulated; lateral surface of thorax smooth or sparsely granulated; forewing membrane brown, cloudy, never

hyaline. ABDOMEN (Fig. 10B): posterior corners of connexiva of abdominal segments 2–4 strongly serrate or dentiform; lateral margins of connexiva of abdominal segments 4–5 sinuous; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 trapezoidal, anterior margin roughly twice as wide as posterior margin. COLORATION (Figs 10A–D): variable; anterior pronotal lobe usually with dark marking; forefemur darkened; corium with a conspicuous transverse band. Female: Large, total length: ~9.12–9.80 mm, width across lateral angles of pronotum: ~3.51–4.19 mm. COLORATION (Figs 10A,B,E): color patterning is generally similar to that of males, but overall lighter in color; forefemur pale, never darkened.

Biology: Specimens have been found on species of Asteraceae and Fabaceae and collected at elevations ranging between 30–2,200 m above sea level.

Distribution: *Phymata mexicana* is distributed from central Mexico to Panama.

Discussion: Based on morphological similarities, *Phymata fasciata panamensis* Kormilev is here synonymized with *P. mexicana*.

Identification remarks: Like *P. fasciata, P. mexicana* also bears (1) a prominent knoblike tubercle of longitudinal pronotal carina, (2) glossy thoracic cuticle, (3) semicircular margin of the anterior pronotal lobe, (4) sinuous lateral margins of connexiva of abdominal segments 4–5, and (6) strongly contrasting markings on the posterior pronotal disk and longitudinal carina. The lateral angles of *P. mexicana*, however, are much more prominent and acute than that of *P. fasciata*. The body color of *P. mexicana* can vary drastically from teneral to mature adults. Males often exhibit very dark (brown to black) pigmentation on their head, thorax, and forelegs.

Type information: Melin's type series of *P. fasciata mexicana* is deposited in the Swedish Museum of Natural History. Only images of a syntype were examined and it is this specimen which we here designate as the lectotype for *P. mexicana*. Having not seen the other syntypes, we are unable to confirm whether they are all conspecific. Kormilev's holotype of *P. fasciata panamensis* was examined and is deposited in the United States National Museum of Natural History in Washington D.C.

LECTOTYPE: (*Phymata mexicana* Melin, 1931): Male: **MEXICO**, Sallé, (UCR_ENT 00123208), (NHRS-GULI000075672) (NRM). Fig. 21I. Image: http://www2.nrm.se/en/het_nrm/f/phymata_fasciatamexicana.html

HOLOTYPE: (*Phymata fasciata panamensis* Kormilev, 1962): Male: **PANAMA:** Canal Zone, Barro Colorado Island, Jul–Aug 1942, Jas. Zetek, (UCR_ENT00008095) (USNM). Fig. 21K.

Additional material examined: See Appendix; 59 specimens, including 28 adult males and 28 adult females.

Phymata mystica Evans, 1931 stat. restit.

Figs 11A–E, 20I. Map 9.

Phymata mystica Evans, 1931

Evans, 1931: p717 (original description)

Phymata fasciata mystica Evans, 1931

Kormilev, 1962: p409 (revision); Henry and Froeschner, 1988: p603 (catalog); Froeschner and Kormilev, 1989: p52 (catalog)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) deep lateral notch, (2) integument lacking elongated setaceous granulation, (3) the prominent, sharply projecting pronotal angles with an exceptionally acute posterior angle that rises nearly to the height/width of the lateral angle, (3) anterior pronotal lobe crenulated and not keeled, and (4) broadly dilated abdomen with laterally expanded connexivum of abdominal segment 5.

Redescription: Male: Medium to large, total length: ~7.73–8.72 mm, width across lateral angles of pronotum: ~3.16–3.43 mm. STRUCTURE: HEAD (Fig. 11A): distiflagellomere of male shorter than pedicel + basiflagellomere. THORAX (Figs 11A,C,D, 20I): thoracic surface matte; anterior pronotal disk without elongated setaceous granulation; posterior pronotal disk punctate; area between lateral pronotal notch and longitudinal carina of the posterior pronotal either with diffuse granulation or devoid of granulation; longitudinal carina with prominent knoblike tubercle; lateral margin of anterior pronotal lobe keeled and semicircular; lateral notch deep; lateral margin of pronotum from lateral notch to lateral angle smooth or with light crenulation; lateral angle prominent and acute; posterior angle prominent and acute; lateral surface of forefemur smooth or sparsely granulated; lateral surface of thorax smooth or sparsely granulated; forewing membrane brown, cloudy, never hyaline. ABDOMEN (Fig. 11B): posterior corners of connexiva of abdominal segments 2–4 strongly serrate or dentiform; lateral margins of connexiva of abdominal segments 4–5 sinuous; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 trapezoidal, anterior margin roughly twice as wide as posterior margin. COLORATION (Figs 11A–D): variable; anterior pronotal lobe usually with dark marking; forefemur pale, never darkened; corium with a conspicuous transverse band. Female: Medium to large, total length: ~8.63–9.67 mm, width across lateral angles of pronotum: ~3.40–3.75 mm. COLORATION (Figs 11A,B,E): with similar color patterns as males but usually lighter-colored overall.

Biology: *Phymata mystica* has been found on *Bidens* L. (Asteraceae), *Solidago* L. (Asteraceae), *Melilotus* Mill. (Fabaceae), and *Ceanothus* L. (Rhamnaceae). Adults can be observed and/or collected year-round. Specimens have been collected at elevations ranging between 2–122 m above sea level.

Distribution: Found primarily in Florida, some specimens have been collected from Alabama (see Clem et al. 2019), Georgia, Louisiana, Mississippi, North Carolina, South Carolina, and Tennessee. This species ranges as far south as the Florida Keys.

Identification remarks: *Phymata mystica* cooccurs with two other *erosa* group taxa with which it may be confused, *P. fasciata* and *P. pennsylvanica*. Additional characters that help separate *P. mystica* from these taxa include: (1) dentiform posterior corners of connexiva of abdominal segments 2–4 (compare with *P. pennsylvanica*), (2) lack of dark pigmentation on the forecoxa and forefemur (compare with male *P. fasciata*), (3) absence of a dense granulation patch on the pronotum mesad to the lateral notch (compare with *P. fasciata*), (4) the knoblike tubercle of the pronotal carina of generally more slender than that of *P. fasciata*, and (5) the lateral and posterior pronotal angles are usually more acute and pronounced than that of these other two species.

Type information: The holotype is deposited in the Illinois Natural History Survey Insect Collection but only the paratypes listed below were examined for this revision.

HOLOTYPE: *Phymata mystica* Evans, 1931: Male: **USA: Florida: *Pinellas Co.:*** Dunedin, 12 Apr 1915, W. S. Blatchley, (INHS).

PARATYPES: **USA: Florida: *Hillsborough Co.:*** Tampa, 28.00000°N, 82.00000°W, Fall 1927, C. O. Bare, 1♀ (UCR_ENT 00070064) (KU). ***St. Johns Co.:*** Saint Augustine, 29.89469°N, 81.31452°W, Nov 11 Jan 12, C. T. Brues, 1♀ (UCR_ENT 00079233) (CAS). **Georgia: *Ware Co.:*** Okefenokee Swamp, Billy's Island, 30.80522°N, 82.34040°W, Jun 1912, Unknown, 2♀ (UCR_ENT 00079231, UCR_ENT 00079232) (CAS).

Additional material examined: See Appendix; 96 specimens, including 54 adult males and 40 adult females.

Phymata obscura Kormilev, 1957 stat. nov.

Figs 12A–E, 20J, 21J. Map 10.

Phymata americana obscura Kormilev, 1957

Kormilev, 1957: p136 (original description); Kormilev, 1962: p472 (revision); Henry and Froeschner, 1988: p602 (catalog); Froeschner and Kormilev, 1989: p45 (catalog)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) lateral notch of medium depth, (2) integument lacking elongated setaceous granulation, (3) absence of granulation patch between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe, (4) transverse band on corium light in color, (5) brownish wing membrane, (6) dark markings along the anterior marginal corners of connexiva of abdominal segments 3–4, (7) rugose posterior pronotal disk, and (8) absence of prominent peaks or protuberances along the longitudinal carinae of the posterior pronotal lobe.

Redescription: Male: Medium to large, total length: ~7.57–8.88 mm, width across lateral angles of pronotum: ~2.90–3.66 mm. STRUCTURE: HEAD (Fig. 12A,D): distiflagellomere of male shorter than pedicel + basiflagellomere. THORAX (Figs 12A,D, 20J): thoracic surface matte; anterior pronotal disk without elongated setaceous granulation; posterior pronotal disk rugose; area between lateral pronotal notch and longitudinal carina of the posterior pronotal either with diffuse granulation or devoid of granulation; longitudinal carina without prominent tubercle; lateral margin of anterior pronotal lobe not keeled; lateral notch of medium depth; lateral margin of pronotum from lateral notch to lateral angle smooth or with light crenulation; lateral angle prominent and acute; posterior angle prominent and acute; lateral surface of forefemur smooth or sparsely granulated; lateral surface of thorax smooth or sparsely granulated; forewing membrane brown, cloudy, never hyaline. ABDOMEN (Fig. 12B): posterior corners of connexiva of abdominal segments 2–4 weakly serrate or dentiform; lateral margins of connexiva of abdominal segments 4–5 sinuous or straight; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 less than twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 rhomboidal, anterior and posterior margin roughly the same width. COLORATION (Figs 12A,B,D): variable; anterior pronotal lobe usually with dark marking; forefemur pale, never darkened; corium with a conspicuous transverse band. Female: Large, total length: ~9.52-10.31 mm, width across lateral angles of pronotum: ~3.31–4.16 mm. COLORATION (Figs 12A,B,C,E): with similar color patterns as males but usually lighter-colored overall.

Biology: *Phymata obscura* has been found on flowers of Asteraceae, Dipsacaceae, Lamiaceae, Rosaceae, and Scrophulariaceae. Specimens have been collected at elevations ranging between 168–1,681 m above sea level.

Distribution: *Phymata obscura* is restricted to the northern Great Basin and Palouse region.

Discussion: This species is often difficult to discern from *P. metcalfi* (which can also be found in Idaho and the northern Great Basin) and *P. americana* (which is found in southern Utah) and is most reliably identified using sequence data. *Phymata obscura* shares close relation to *P. metcalfi* and *P. arctostaphylae* (Masonick and Weirauch, 2020).

Identification remarks: These characters in particular help to distinguish *P. obscura* from *P. americana* and *P. metcalfi*: (1) rugose posterior pronotal disk (disk punctate in *P. americana* and *P. metcalfi*), (2) absence of prominent peaks or protuberances along the longitudinal carinae of the posterior pronotal lobe (present in western populations of *P. americana*), (3) connexivum of abdominal segment 5 not abruptly dilated in males (abdomen may appear dilated at connexivum of abdominal segment 5 in some western *P. americana* specimens), and (4) brownish wing membrane (usually hyaline in *P. metcalfi*).

Type information: Kormilev's holotype was examined and is deposited in the United States National Museum of Natural History in Washington D.C.
HOLOTYPE: *Phymata obscura* Kormilev, 1957: Male: **USA: Idaho:** Moscow, 18 Aug 1940, T. A. Brindley, (UCR_ENT 00008091) (USNM). Fig. 21J.

Additional material examined: See Appendix; 179 specimens, including 121 adult males and 58 adult females.

Phymata pacifica Evans, 1931

Figs 13A–E, 20K, 21O. Map 11.

Phymata pacifica Evans, 1931
Evans, 1931: p725 (original description); Kormilev, 1962: p422 (revision); Henry and Froeschner, 1988: p603 (catalog); Froeschner and Kormilev, 1989: p56 (catalog)

Phymata pacifica pacifica Evans, 1931
Kormilev, 1962: p422 (revision); Henry and Froeschner, 1988: p603 (catalog); Froeschner and Kormilev, 1989: p56 (catalog)

Phymata pacifica hainesi Kormilev, 1962 syn. nov.
Kormilev, 1962: p424 (original description); Froeschner and Kormilev, 1989: p56 (catalog)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) deep lateral notch, (2) integument lacking elongated setaceous granulation, (3) prominent granulation patch on the pronotum mesad to the lateral notch, (4) relatively small size (~6.5–8.5 mm), and (5) posterior lateral corners of connexiva of abdominal segments 2–5 weakly dentiform.

Redescription: Male: Small to medium, total length ~6.40–6.76 mm, width across lateral angles of pronotum: ~2.57–2.75 mm. STRUCTURE: HEAD (Fig. 13A,D): distiflagellomere of male shorter than pedicel + basiflagellomere. THORAX (Figs 13A,D, 20K): thoracic surface matte; anterior pronotal disk without elongated setaceous granulation; posterior pronotal disk punctate; area between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe with a distinct granulation patch; longitudinal carina with prominent knoblike tubercle; lateral margin of anterior pronotal lobe not keeled and semicircular; lateral notch deep; lateral margin of pronotum from lateral notch to lateral angle smooth or with light crenulation; lateral angle prominent and acute; posterior angle small and obtuse; lateral surface of forefemur smooth or sparsely granulated; lateral surface of thorax granulated; forewing membrane hyaline. ABDOMEN (Fig. 13B): posterior corners of connexiva of abdominal segments 2–4 inconspicuous/subtle; lateral margins of connexiva of abdominal segments 4–5 sinuous; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 less than twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 rhomboidal, anterior and posterior margin roughly the same width. COLORATION (Figs 13A,B,D): variable; anterior pronotal lobe sometimes with a reddish-brown marking; forefemur pale, never darkened; corium with a conspicuous transverse band that is often pinkish or lavender in color. Lateral surface of head and thorax, legs, connexiva of abdominal segments 2–4 and 6–7, and ventral surface of body may be ivory, pale green, or yellowish; the darker markings on the dorsum of the head, pronotum, corium, and connexivum of abdominal segment 5 (and sometimes the anterolateral corner of connexivum of abdominal segment 4) are usually reddish-brown to black. Female: Small to medium, total length: ~7.18–8.77 mm, width across lateral angles of pronotum: ~2.96–3.40 mm. COLORATION (Figs 13A,B,C,E): Body predominantly ivory to pale-green or yellow in color with pink to reddish-brown markings on the dorsum of the head, pronotum, corium, and connexivum of abdominal segment 5.

Biology: *Phymata pacifica* is common in coastal sage scrub and chaparral communities of coastal California and the Baja Peninsula. While this species has been found on a variety of plants, it is frequently encountered on blooming *Eriogonum fasciculatum* Benth. Like many ambush bugs, *P. pacifica* is a generalist predator that preys on a broad range of flower visiting arthropods. Molecular evidence suggests that *P. pacifica* frequently engages in intraguild predation by consuming beetles, parasitoid wasps and flies, crab spiders, and other predatory true bugs (Masonick et al. 2019). Adults are relatively common from June through September and may be found living in sympatry with *P. metcalfi* and *P. paraborica* sp. nov. Specimens have been collected at elevations ranging between 4–1,997 m above sea level.

Distribution: Restricted to California and the Baja California Peninsula.

Discussion: We here treat the nominate subspecies and *P. pacifica hainesi* Kormilev as *P. pacifica*. The third subspecies previously recognized, *P. pacifica stanfordi* Evans, is elevated to species rank in this revision based

on molecular evidence, its divergent morphology, and cooccurrence with *P. pacifica*. Populations in Baja California often are much darker in color than those that occur in California.

Identification remarks: The following attributes can help distinguish *P. pacifica* from other western taxa: (1) rounded anterior pronotal lobe (compare with the relatively flatter anterior pronotal lobe of *P. luteomarginata* and *P. paraborica* sp. nov.), (2) relatively weak posterior pronotal angle (see prominent posterior pronotal angle of *P. metcalfi* or *P. stanfordi*), (3) brown wing membrane (compare with the hyaline wing membranes *P. luteomarginata* or *P. metcalfi*), and (4) body overall usually ivory in color with reddish-brown to black markings on head and pronotum and a pink or lavender transverse band on the corium.

Type information: Evans' holotype of *P. pacifica* is housed at the University of Kansas Biodiversity Institute but only a selection of his paratypes were examined for this revision. Kormilev's holotype of *P. pacifica hainesi* was examined and is deposited at the United States National Museum of Natural History in Washington D.C.

HOLOTYPE: (*Phymata pacifica* Evans, 1931): Male: **USA: California:** ***San Diego CO.:*** 04 Jul 1929, R. H. Beamer, (KU).

PARATYPES: (*Phymata pacifica* Evans, 1931): **USA: California:** ***Marin Co.:*** Mount Tamalpais, 37.90389°N, 122.59500°W, no date provided, Unknown, 1♂ (UCR_ENT 00086560) (LACM). ***Orange Co.:*** Orange County, no specific locality, 33.74430°N, 117.87407°W, 14 Jul 1929, R. H. Beamer, 1♀ (UCR_ENT 00070067) (KU). ***San Diego Co.:*** San Diego County, 32.71528°N, 117.15639°W, 04 Jul 1929, R. H. Beamer, 1♂ (UCR_ENT 00070066) (KU).

HOLOTYPE: (*Phymata pacifica hainesi* Kormilev, 1962): Male: **MEXICO: Baja California:** Calamajué (as Calamujuet), May 1889, C. D. Haines, (UCR_ENT 00008102) (USNM). Fig. 21O.

Additional material examined: See Appendix; 932 specimens, including 531 adult males and 386 adult females.

Phymata paraborica sp. nov.

Figs 14A–E, 20L. Map 12.

urn:lsid:zoobank.org:act:6BCE48A2-BD0D-47F2-A514-9201D79B28CC

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) shallow lateral notch, (2) posterior pronotal angle conspicuous and right, (3) very short and blunt frontal process, and (4) flattened anterior pronotal disk that is usually very smooth overall and without raised tubercles along the posterior margin.

Description: Male: Small to medium, total length ~6.59–7.15 mm, width across lateral angles of pronotum: ~2.38–2.66 mm. STRUCTURE: HEAD (Fig. 14A,C,D): distiflagellomere of male shorter than pedicel + basiflagellomere. THORAX (Figs 14A,C,D, 20L): thoracic surface matte; anterior pronotal disk without elongated setaceous granulation; posterior pronotal disk punctate; area between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe usually with a small granulation patch; longitudinal carina without prominent tubercle; lateral margin of anterior pronotal lobe not keeled and inconspicuous; lateral notch shallow; lateral margin of pronotum from lateral notch to lateral angle smooth or with light crenulation; lateral angle small and obtuse; posterior angle prominent and right; lateral surface of forefemur smooth or sparsely granulated; lateral surface of thorax smooth or sparsely granulated; forewing membrane brown, cloudy, never hyaline. ABDOMEN (Fig. 14B): posterior corners of connexiva of abdominal segments 2–4 inconspicuous/subtle; lateral margins of connexiva of abdominal segments 4–5 convex; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 less than twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 rhomboidal, anterior and posterior margin roughly the same width. COLORATION (Figs 14A–D): variable; anterior pronotal lobe usually with dark marking; forefemur pale, never darkened; corium with a conspicuous transverse band (usually pink or purple in color); body overall usually pale yellow or greenish with dark brown or black markings. Female: Small to medium, total length: ~6.89–7.94 mm, width across lateral angles of pronotum: ~2.47–2.88 mm. COLORATION (Figs 14A,B,E): very similar to that of males.

Etymology: Named for its resemblance to *P. borica* Evans, a species native to the Colorado Plateau region of the United States.

Biology: *Phymata paraborica* has been collected from *Eriogonum fasciculatum* Benth. (Polygonaceae) and *Adenostoma* Hook. & Arn. (Rosaceae) in scrublands and chaparral habitats.

Distribution: This species is found along the Transverse Ranges of southern California.

Discussion and identification remarks: This species is sympatric with *P. pacifica* and can be found on the same host plants (i.e., *E. fasciculatum*). *Phymata paraborica* sp. nov. has a more diffuse granulation patch, flatter lateral margin of the anterior pronotal lobe, shallower lateral notch, obtuse or right lateral angle (compare with acute lateral angle of *P. pacifica*) and is overall much darker than *P. pacifica*. These additional characteristics help separate *P. paraborica* sp. nov. from other Californian taxa: (1) the small to medium size, (2) lateral margin of anterior pronotal lobe smooth (compare with crenulated margin of *P. luteomarginata*), (3) both sexes often with blackened head and pronotum (never black in *P. luteomarginata* females), and (4) brown forewing membrane (compare with hyaline membrane of *P. luteomarginata* or *P. metcalfi*).

Type information: The holotype and allotype of this new species have been deposited in the University of California Riverside Entomology Research Museum, Riverside, CA, USA. In total, 79 specimens, comprising 39 adult males and 40 adult females were designated as types.

HOLOTYPE: Male: **USA: California:** ***San Bernardino Co.:*** San Bernardino National Forest, Lytle Creek Road, 34.26668°N, 117.51085°W, 08 Jul 2016, C. Weirauch, P. Masonick, & M. Hernandez, (UCR_ENT 00127618) (UCR). NOTE: The specimen's left foretarsus is missing and the right hind leg was removed for DNA extraction.

ALLOTYPE: Female: **USA: California:** ***San Bernardino Co.:*** San Bernardino National Forest, Lytle Creek Road, 34.26668°N, 117.51085°W, 08 Jul 2016, C. Weirauch, P. Masonick, & M. Hernandez, (UCR_ENT 00127609) (UCR). NOTE: The specimen's right hind leg was removed for DNA extraction.

PARATYPES: **USA: California:** ***Los Angeles Co.:*** Crystal Lake, 34.31940°N, 117.84700°W, 27 Jul 1968, Unknown, 1♀ (UCR_ENT 00061717) (UCR). Mt. Wilson, 34.22389°N, 118.06028°W, 13 Jul 1940, G. P. Mackenzie, 1♂ (UCR_ENT 00061612) (UCR). N6 towards Devil's Punchbowl, 34.44081°N, 117.89247°W, 22 Aug 2014, C. Weirauch, A. Knyshov, P. Masonick, 1♀ (UCR_ENT 00104936) (UCR). San Gabriel Mountains: Tie Canyon and area, 34.39944°N, 118.07618°W, 23 Jun 1967, R. H. Crandall, 1♀ (UCR_ENT 00039343) (LACM). South Fork Campground, 34.39444°N, 117.81944°W, 06 Sep 1971, J. A. Honey, 1♂ (UCR_ENT 00039342) (LACM). Tanbark Flats, San Gabriel Mountains, 34.20350°N, 117.76105°W, 22 Jun 1950, W. A. McDonald, 5♂ (UCR_ENT 00039317-UCR_ENT 00039321), 6♀ (UCR_ENT 00039322-UCR_ENT 00039326, UCR_ENT 00039328) (LACM); 22 Jun 1950, D. C. Blodget, 1♂ (UCR_ENT 00039327) (LACM); 25 Jun 1950, D. C. Blodget, 1♂ (UCR_ENT 00039329), 2♀ (UCR_ENT 00039337, UCR_ENT 00039338) (LACM); 25 Jun 1950, F. X. Williams, 1♂ (UCR_ENT 00079052), 1♀ (UCR_ENT 00079061) (CAS); 21 Jun 1950, J K Windsor, 1♂ (UCR_ENT 00039330) (LACM); 25 Jun 1952, B. Tinglof, 1♂ (UCR_ENT 00039331) (LACM); 23 Jun 1950, J K Windsor, 3♂ (UCR_ENT 00039332-UCR_ENT 00039333, UCR_ENT 00039340), 1♀ (UCR_ENT 00039334) (LACM); 08 Jul 1950, J K Windsor, 1♀ (UCR_ENT 00039335) (LACM); 08 Jul 1952, Unknown, 1♂ (UCR_ENT 00039336) (LACM); 30 Jun 1950, W. A. McDonald, 1♀ (UCR_ENT 00039339) (LACM); 13 Jul 1950, J K Windsor, 1♀ (UCR_ENT 00039341) (LACM). ***Orange Co.:*** Arch Beach, 33.52169°N, 117.76477°W, 02 Jul 1925, L. J. Muchmore, 1♂ (UCR_ENT 00039345) (LACM). ***Riverside Co.:*** 12 mi E of Hemet, San Bernardino National Forest, 33.70871°N, 116.76110°W, 26 May 2009, C. Weirauch, D. Forero, G. Zhang, 2♂ (UCR_ENT 00071890, UCR_ENT 00071897), 3♀ (UCR_ENT 00071888-UCR_ENT 00071889, UCR_ENT 00071896) (UCR). Cleveland National Forest, 33.50972°N, 117.36694°W, 19 Apr 2015, Unknown, 1♀ (UCR_ENT 00127544) (UCR). Gavilan, 33.81000°N, 117.35800°W, 09 Jun 1960, Timberlake, 1♂ (UCR_ENT 00066290) (UCR). Reche Canyon Road, 33.98228°N, 117.21548°W, 08 Jul 2015, A. J. Mayor, 1♀ (UCR_ENT 00123231) (UCR). Santa Rosa Mountains, 33.52417°N, 117.27528°W, 01 Jun 1958, C. Cushner, 1♂ (UCR_ENT 00079289) (CAS). ***San Bernardino Co.:*** 3 mi S Camp Angelus, 34.10231°N, 116.98167°W, 06 Jul 1960, W. F. Barr, 1♂ (UCR_ENT 00079900) (WFBM). 6 mi NW of Cajon, 34.35424°N, 117.52920°W, 23 Jun 1958, W. F. Barr, 1♂ (UCR_ENT 00079899) (WFBM). Camp Baldy, 34.29528°N, 116.91392°W, 14 Jun 1926, L. L. Muchmore, 5♂ (UCR_ENT 00096290-UCR_ENT 00096293, UCR_ENT 00096297), 1♀ (UCR_ENT 00096298) (LACM); 12 Jun 1916, L. J. Muchmore, 1♂ (UCR_ENT 00096294), 2♀ (UCR_ENT 00096295, UCR_ENT 00096296) (LACM). Hwy. 138, W of Silverwood Lake, 34.29038°N, 117.34930°W, 31 May 2015, A. J. Mayor, 1♂ (UCR_ENT 00123286) (UCR). Miller Canyon, 34.28417°N, 117.32972°W, 24 Jul 1941, W. F. Barr, 1♀ (UCR_ENT 00079901) (WFBM). San Bernardino National Forest, E of Silverwood Lake State Rec. Area, 34.27183°N, 117.30053°W, 28 Jun 2012, Schuh and Weirauch, 1♀ (UCR_ENT 00071908) (UCR). San Bernardino National Forest, Hwy 38, Mill Creek Canyon, 34.09690°N, 116.96510°W, 29 May 2017, P. Masonick, 1♂ (UCR_ENT 00127547) (UCR). San Bernardino National Forest, Lytle Creek Road, 34.26668°N, 117.51085°W, 08 Jul 2016, C. Weirauch, P. Masonick, M. Hernandez, 4♂ (UCR_ENT 00127616-UCR_ENT 00127627, UCR_ENT 00127619-UCR_ENT 00127620), 6♀ (UCR_ENT 00127545, UCR_ENT 00127610-UCR_ENT 00127614) (UCR); 26 Jun 2016, P. Masonick & C. Dodge, 1♀ (UCR_ENT 00127615) (UCR); 26 Jul 2016, P. Masonick, M. Hernandez, 1♂ (UCR_ENT 00127626) (UCR). Valley of the Falls Drive: large pullout east of the Hwy 38 / Valley of the Falls Drive junction, 34.09490°N, 116.94720°W, 29 Aug 2014, P. Masonick, S. Frankenberg, A. Michael, 2♀ (UCR_ENT 00104976, UCR_ENT 00104979) (UCR). Wrightwood, 34.36083°N, 117.63250°W, 06 Jul 1963, D. S. Verity, 1♂ (UCR_ENT 00039344) (LACM). ***San Diego Co.:*** Indian Springs, 32.72033°N, 116.88085°W, 19 Jun 1927, C. C. Searl, 1♂ (UCR_ENT 00078900) (SDNH). Pine Valley, 32.83583°N, 116.53361°W, 22 Aug 1927, F. W. Kelsey, 1♀ (UCR_ENT 00078908) (SDNH). ***Santa Barbara Co.:*** Santa Ynez Mountains, W. Camino Cielo Rd., 34.52720°N, 119.98047°W, 18 Jul 2015, A.J. Mayor & M. Gimmel, 2♀ (UCR_ENT 00123193, UCR_ENT 00123240) (UCR). ***Ventura Co.:*** Lockwood Valley, 34.74167°N, 119.08555°W, 29 Jun 1972, Unknown, 1♀ (UCR_ENT 00066879) (UCR).

Phymata pennsylvanica Handlirsch, 1897

Figs 15A–F, 20M, 21E, 22A–C. Map 13.

Phymata erosa pennsylvanica Handlirsch, 1897
Handlirsch, 1897: p163 (original description)

Phymata americana newyorkensis Melin, 1931
Melin, 1931: p7 (original description); Evans, 1931: p714 (synonym)

Phymata pennsylvanica Handlirsch, 1897
Kormilev, 1953: p63 (taxonomy); Kormilev, 1962: p394 (revision); Henry and Froeschner, 1988: p603 (catalog); Froeschner and Kormilev, 1989: p56 (catalog)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) lateral notch of medium depth, (2) integument lacking elongated setaceous granulation, (3) lateral margin of anterior pronotal lobe never keeled, (4)

lateral and posterior pronotal angles prominent and often acute, (5) posterior pronotal disk punctate, (6) connexiva of abdominal segments 3–4 pale, usually without dark marginal spots, (7) lateral margins of connexiva of abdominal segments 4–5 more or less straight, and (8) wing membrane brownish.

Redescription: Male: Medium to large, total length: ~7.73–8.67 mm, width across lateral angles of pronotum: ~2.75–3.09 mm. STRUCTURE: HEAD (Fig. 15B): distiflagellomere longer than pedicel + basiflagellomere (dflg : pd + bflg = ~1.15). THORAX (Figs 15A,B,E, 20M): thoracic surface matte; anterior pronotal disk without elongated setaceous granulation; posterior pronotal disk punctate; area between lateral pronotal notch and longitudinal carina of the posterior pronotal either with diffuse granulation or devoid of granulation; longitudinal carina without prominent tubercle; lateral margin of anterior pronotal lobe not keeled; lateral notch of medium depth; lateral margin of pronotum from lateral notch to lateral angle smooth or with light crenulation; lateral angle prominent and acute; posterior angle prominent and acute; lateral surface of forefemur smooth or sparsely granulated; lateral surface of thorax smooth or sparsely granulated; forewing membrane brown, cloudy, never hyaline. ABDOMEN (Fig. 15C): posterior corners of connexiva of abdominal segments 2–4 inconspicuous/subtle; lateral margins of connexiva of abdominal segments 4–5 concave or straight; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 trapezoidal, anterior margin roughly twice as wide as posterior margin. COLORATION (Figs 15A–E): head (dorsal and lateral surfaces), distiflagellomere, pronotum, scutellum, and entire connexivum of abdominal segment 5 and anterior portion of connexivum of abdominal segment 6 are usually dark brown to black and mostly uniform in color, the pronotum sometimes bears a narrow light-colored marking along the margin of the lateral notch; forefemur never darkly pigmented; corium with a dark transverse band (sometimes reddish-brown or purplish) that faintly contrasts with the rest of the corium; lateral thoracic surface divided into distinct dark-colored (dorsal) and light-colored (ventral) regions (contrast with *P. americana*); connexiva of abdominal segments 3–4 usually without dark basal spots (this character is plastic as many northern populations do exhibit basal spots like *P. americana*); spiracle of abdominal segment 6 usually surrounded by dark pigmentation. NOTE: While the legs, connexiva of abdominal segments 2–4 and 6–7, and overall ventral surfaces of live specimens tend to be lime-green or bright yellow, these colors quickly fade to drab yellow or beige on specimens that are pinned or preserved in alcohol. The eyes of live males are also usually orange or reddish in color. Female: Large, total length: ~8.97–9.55 mm, width across lateral angles of pronotum: 3.16–3.50 mm. STRUCTURE: HEAD (Fig. 15A): distiflagellomere relatively long, only slightly shorter than pedicel + basiflagellomere (dflg : pd + bflg = ~0.88). COLORATION (Figs A,C,D,F): pronotum mostly reddish-brown to chestnut in color and never as dark as in males; lateral surface of the body is similar in pattern to that of males, however, is generally lighter brown and never black; the transverse corial band ranges from beige to chestnut brown; lateroventral surface of abdominal sternites 5–7 sometimes with faint or diffuse brown coloration.

Biology: Males are often seen mate guarding females. This species is found on a variety of plants but perhaps is most frequently encountered on Asteraceae. Specimens have been collected at elevations ranging between 3–1,158 m above sea level.

Distribution: *P. pennsylvanica* is found primarily east of the Mississippi River and is very common during summer months. It ranges from southern Canada across New England and Appalachia south into Florida and west over the Ozark Plateau.

Discussion: This species is slightly smaller than *P. americana*, the species with which it is most likely to be confused. The ranges of these two species are largely parapatric and overlap in New England and the Great Lakes region (see Swanson 2013). See discussion section of *P. americana* for additional information pertaining to these two species.

Identification remarks: A combination of these additional characteristics may help separate *P. pennsylvanica* from *P. americana*: (1) a distiflagellomere that is in males distinctly longer than the scape and basiflagellomere combined or in females roughly subequal in length, (2) pronotum mostly uniform in color (black in males and brown in females), (3) corium with a subtle, dark transverse band (this band is very conspicuous in *P. americana*), (4) absence of dark markings along anterior margins of connexiva of abdominal segments 3–4, (5) relatively smooth anterior margins of connexiva of abdominal segments 2–4, (6) abruptly dilated connexivum of abdominal segment 5 in males (abdomen of both sexes appearing more diamond shaped when viewed dorsally), (7) lateral thoracic surface divided into distinct dark-colored (dorsal) and light-colored (ventral) regions, (8) dark pigmentation that usually encircles the spiracles of abdominal segments 5 and 6, and (9) the general lack of diffuse granulation on the pronotum between the lateral notch and longitudinal carina. Lastly, while *P. pennsylvanica* usually bears well developed preocellar and ocellar processes, these structures are often shorter and less branched than those

of *P. americana*.

Type information: Handlirsch only selected syntypes for ambush bug species he described. The syntype series of *P. pennsylvanica* is housed at the Natural History Museum Vienna and was cataloged by Rabitsch (2000). We here designate one of these specimens to serve as a lectotype. Images of a syntype of *Phymata americana newyorkensis* Melin, 1931 were also examined.

LECTOTYPE: Male: USA: Pennsylvania: H. G. Klages (UCR_ENT 00075081) (NHMW). Fig. 22A–C.

SYNTYPE: (*Phymata americana newyorkensis* Melin, 1931): Male: (NRM). Fig. 21E. Image: http://www2.nrm.se/en/het_nrm/a/phymata_americananewyorkensis.html

Additional material examined: See Appendix; 123 specimens, including 69 adult males and 54 adult females.

Phymata rossi Evans, 1931

Figs 16A–E, 20N, 21M. Map 14.

Phymata rossi Evans, 1931

Evans, 1931: p270 (original description); Kormilev, 1962: p395 (revision); Henry and Froeschner, 1988: p604 (catalog); Froeschner and Kormilev, 1989: p58 (catalog)

Phymata granulosa texasana Kormilev, 1957 syn. nov.

Kormilev, 1957: p134 (original description); Henry and Froeschner, 1988: p603 (catalog); Froeschner and Kormilev, 1989: p53 (catalog)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) elongated setaceous granulation on the head and thorax, (2) crenulated margin of the pronotum and connexiva, and (3) sepia or rosette colored body, the lateral and ventral surfaces of which and the legs often with a pinkish blush.

Redescription: Male: Small to medium, total length ~6.59–8.0 mm, width across lateral angles of pronotum: ~2.61–3.18 mm. STRUCTURE: HEAD (Fig. 16A,D): distiflagellomere of male shorter than pedicel + basiflagellomere. THORAX (Figs 16A,D, 20N): thoracic surface matte; anterior pronotal disk with elongated setaceous granulation; posterior pronotal disk punctate; area between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe with a distinct granulation patch; longitudinal carina with prominent tubercle bearing elongated granules; lateral margin of anterior pronotal lobe not keeled; lateral notch of medium depth; lateral margin of pronotum from lateral notch to lateral angle heavily crenulated with prominent tubercles; lateral angle prominent and acute; posterior angle prominent and acute; lateral surface of forefemur heavily granulated; lateral surface of thorax heavily granulated; forewing membrane brown, cloudy, never hyaline. ABDOMEN (Fig. 16B): posterior corners of connexiva of abdominal segments 2–4 weakly serrate or dentiform; lateral margins of connexiva of abdominal segments 4–5 sinuous; lateral margins of connexiva of abdominal segments 3–6 rough, crenulated / heavily granulated; connexivum of abdominal segment 5 less than twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 rhomboidal, anterior and posterior margin roughly the same width. COLORATION (Figs 16A–D): variable; anterior pronotal lobe usually with dark marking; forefemur sepia to rosette in color, never black; corium with a conspicuous sepia to rosette transverse band. Female: Medium, total length: ~8.21–8.82 mm, width across lateral angles of pronotum: ~3.12–3.38 mm. COLORATION (Figs 16A,B,E):

Biology: *Phymata rossi* has been found on *Asclepias* L., *Helianthus* L., *Sphaeralcea* A. St.-Hil., *Ligustrum* L., *Purshia* DC. ex Poir., several genera of Fabaceae including *Cassia* L., *Melilotus* Mill., *Mimosa* L., and *Prosopis* L., and *Quercus* L (Fagaceae). Specimens have been collected at elevations ranging between 574–1,839 m above sea level.

Distribution: While the majority of *P. rossi* species examined were collected in Arizona, this species has also been found in California, New Mexico, Texas, and Utah.

Discussion: *Phymata rossi*, as well as *P. granulosa* and *P. salicis*, are the only *erosa* group taxa that have extensive elongated setaceous granulation on their head and thorax. Molecular evidence indicates that *P. rossi* is closely related to sympatric *P. borica*. Since the holotype of *P. granulosa texasana* Kormilev bears a lateral pronotal margin more like that of *P. rossi* than *P. granulosa* (e.g., has a very acute lateral angle that is directed posteriorly), lacks a darkly colored forefemur, and occurs closer to the documented distribution of *P. rossi* than *P. granulosa*, we here synonymize *P. granulosa texasana* Kormilev with the former. Some populations display differences in the degree of setaceous granulation covering the body.

Identification remarks: In the southwestern United States, *P. saileri* is the only other species of the *erosa* group that also bears conspicuous elongated setaceous granulation on the head and thorax. *Phymata rossi* is generally much lighter in color than *P. saileri* and lacks a glossy cuticle.

Type information: Evans' holotype is deposited in the University of Kansas Biodiversity Institute, but only a paratype from the same collection was examined for this revision. Kormilev's holotype of *P. granulosa texasana* was examined and is deposited in the United States National Museum of Natural History in Washington D.C.

HOLOTYPE: (*Phymata rossi* Evans, 1931): ♂, **USA: Arizona: *Cochise Co.:*** Huachuca Mountains, 08 Aug 1927, R.H. Beamer, (KU).

PARATYPE: (*Phymata rossi* Evans, 1931): **USA: Arizona: *Cochise Co.:*** Huachuca Mountains, 31.50200°N, 110.39940°W, 01 Aug 1927, R. H. Beamer, 1♀ (UCR_ENT 00070062) (KU).

HOLOTYPE: (*Phymata granulosa texasana* Kormilev, 1957): ♂,

USA: Texas: Chisos Mountains, 09 Jul 1936, J.N. Knull, (UCR_ENT 00008097), (USNM). Fig. 21M.

Additional material examined: See Appendix; 106 specimens, including 62 adult males and 38 adult females.

Phymata saileri Kormilev, 1957

Figs 17A–E, 20O, 21P. Map 15.

Phymata saileri Kormilev, 1957

Kormilev, 1957: p133 (original description); Kormilev, 1962: p472 (revision); Henry and Froeschner, 1988: p604 (catalog); Froeschner and Kormilev, 1989: p58 (catalog)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) abundance of setaceous granulation on thorax and forefemur, (2) strongly crenulated pronotal and connexival margins, and (3) the darkened (black or brown) head, thorax, and forelegs of both males and females.

Redescription: Male: Medium to large, total length: ~8.01 mm, width across lateral angles of pronotum: ~2.86 mm. STRUCTURE: HEAD (Fig. 17A): distiflagellomere of male shorter than pedicel + basiflagellomere. THORAX (Figs 17A,C,D, 20O): thoracic surface glossy; anterior pronotal disk with elongated setaceous granulation; posterior pronotal disk rugose; area between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe with a distinct granulation patch; longitudinal carina with prominent knoblike tubercle; lateral margin of anterior pronotal lobe keeled and regular; lateral notch of medium depth; lateral margin of pronotum from lateral notch to lateral angle heavily crenulated with prominent tubercles; lateral angle prominent and acute; posterior angle prominent and acute; lateral surface of forefemur heavily granulated; lateral surface of thorax heavily granulated; forewing membrane brown, cloudy, never hyaline. ABDOMEN (Fig. 17B): posterior corners of connexiva of abdominal segments 2–4 strongly serrate or dentiform; lateral margins of connexiva of abdominal segments 4–5 sinuous; lateral margins of connexiva of abdominal segments 3–6 heavily granulated; connexivum of abdominal segment 5 twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 trapezoidal, anterior margin roughly twice as wide as posterior margin. COLORATION (Figs 17A,B,D): variable; anterior pronotal lobe usually with dark marking; forefemur darkened; corium with a conspicuous transverse band. Female: Medium, total length: ~8.08 mm, width across lateral angles of pronotum: ~3.03 mm. COLORATION (Figs 17A,B,C,E): very similar to that of male with forefemur darkened brown or black

Biology: This rare species is endemic to the Chihuahuan Desert and has been found on blooming acacia (*Senegalia* Raf.). Specimens have been collected at elevations ranging between 1,411–1,579 m above sea level.

Distribution: This species has been collected in Arizona.

Discussion: *Phymata saileri* is the only species of the Nearctic *erosa* group where both the male and female have almost completely darkened lateral surfaces of head and thorax and black forelegs. It should be noted that the specimen of *P. saileri* reported by Swanson (2019) from Sierra County, New Mexico should actually be referred to as *P. rossi* (Swanson, pers. comm. 2020).

Identification remarks: These additional characters help to separate *P. saileri* from other desert taxa: (1) glossy cuticle of the pronotum, (2) rugose posterior pronotal disc, (3) posteriorly directed lateral and posterior pronotal angles, and (4) sinuous margin of connexivum of abdominal segment 5.

Type information: Kormilev's holotype was examined and is deposited in the United States National Museum of Natural History in Washington D.C.

HOLOTYPE: ♀, **USA: Arizona:** Oracle, 29 Jun [year not indicated], (UCR_ENT 00008105), (USNM). Fig. 21P.

Additional material examined: See Appendix; 3 specimens, 1 adult male and 2 adult females.

Phymata salicis Cockerell, 1900

Figs 18A–D, 20P, 21Q. Map 16.

Phymata erosa salicis Cockerell, 1900

Cockerell, 1900: p66 (original description)

Phymata salicis Cockerell, 1900

Evans, 1931: p723 (taxonomy); Kormilev, 1962: p419 (revision); Henry and Froeschner, 1988: p604 (catalog); Froeschner and Kormilev, 1989: p58 (catalog)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) shallow lateral notch, (2) absence of dark pigmentation along the margin of the anterior pronotal lobe, (3) relatively small size and narrow body, and (4) greatly reduced posterior angle.

Redescription: Male: Medium, total length ~7.77–8.15 mm, width across lateral angles of pronotum: ~2.69–2.85 mm. STRUCTURE: HEAD (Fig. 18A,C): distiflagellomere of male shorter than pedicel + basiflagellomere. THORAX (Figs 18A,C, 20P): thoracic surface matte to glossy; anterior pronotal disk without elongated setaceous granulation; posterior pronotal disk punctate; area between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe either with a small granulation patch or no granulation; longitudinal carina without prominent tubercle; lateral margin of anterior pronotal lobe not keeled and inconspicuous; lateral notch shallow; lateral margin of pronotum from lateral notch to lateral angle smooth or with light crenulation; lateral angle small and obtuse;

posterior angle inconspicuous; lateral surface of forefemur smooth or sparsely granulated; lateral surface of thorax smooth or sparsely granulated; forewing membrane brown, cloudy, never hyaline. ABDOMEN (Fig. 18B): posterior corners of connexiva of abdominal segments 2–4 inconspicuous/subtle; lateral margins of connexiva of abdominal segments 4–5 concave or straight; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 less than twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 rhomboidal, anterior and posterior margin roughly the same width. COLORATION (Figs 18A–C): variable; anterior pronotal lobe never with dark marking; forefemur pale, never darkened; corium without obvious transverse band. Female: Medium, total length: ~8.01–9.00 mm, width across lateral angles of pronotum: ~2.71–3.04 mm. COLORATION (Figs 18A,B,D): Similar to that of male but generally lighter overall.

Biology: *Phymata salicis* is associated with riparian habitats along the Colorado River and its tributaries. It has been collected from species of *Salix* L. (Salicaceae), and several species of riparian associated Asteraceae including *Baccharis salicifolia* (Ruiz & Pav.) Pers., *Chloracantha spinosa* (Benth.) G. L. Nesom, and *Pluchea sericea* (Nutt.) Coville. Specimens have been collected at elevations ranging between -50–650 m above sea level.

Distribution: *Phymata salicis* is found in the southwestern United States in riparian habitats along the Colorado River and its tributaries. Restricted to Arizona, southern Nevada, and California.

Discussion and identification remarks: This rare species can be distinguished from other desert taxa using pronotal morphology and color. Individuals vary from being a uniform pale yellow or green in color to having disruptive color patterning with dark brown markings on the head, pronotum, and abdomen. The corium might have whitish or pinkish markings.

Type information: Cockerell's type of *P. salicis* was examined and is deposited in the United States National Museum of Natural History in Washington D.C.

HOLOTYPE: ♀, **USA: Arizona:** Phoenix, 07 Oct 1899, T. D. A. Cockerell, ex: *Salix* (UCR_ENT 00008068), (USNM). Fig. 21Q.

Material examined: See Appendix; 23 specimens, including 13 adult males and 9 adult females.

Phymata stanfordi Evans, 1931 stat. nov.

Figs 19A–E, 20Q. Map 17.

Phymata pacifica stanfordi Evans, 1931

Evans, 1931: p726 (original description); Kormilev, 1962: p424 (revision); Henry and Froeschner, 1988: p603 (catalog); Froeschner and Kormilev 1989: p56 (catalog)

Diagnosis: Recognized from other species of the Nearctic *erosa* group by the following combination of characters: (1) lateral notch of medium depth, (2) integument lacking elongated setaceous granulation but with extensive fine granulation across much of the body, (3) diffuse granulation between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe, (4) punctate posterior pronotal disk, (5) lateral and posterior angles prominent and acute, and (6) forewing membrane usually hyaline.

Redescription: Male: Small to medium, total length: ~7.03–8.13 mm, width across lateral angles of pronotum: ~2.61–2.92 mm. STRUCTURE: HEAD (Fig. 19A,D): distiflagellomere of male shorter than pedicel + basiflagellomere. THORAX (Figs 19A,D, 20Q): thoracic surface matte; anterior pronotal disk without elongated setaceous granulation; posterior pronotal disk punctate; area between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe with diffuse granulation; longitudinal carina without prominent tubercle; lateral margin of anterior pronotal lobe not keeled; lateral notch of medium depth; lateral margin of pronotum from lateral notch to lateral angle with light crenulation; lateral angle prominent and acute; posterior angle prominent and acute; lateral surface of forefemur smooth or sparsely granulated; lateral surface of thorax finely granulated; forewing membrane hyaline or slightly cloudy. ABDOMEN (Fig. 19B): posterior corners of connexiva of abdominal segments 2–4 weakly serrate or dentiform; lateral margins of connexiva of abdominal segments 4–5 sinuous; lateral margins of connexiva of abdominal segments 3–6 with or without fine granulation; connexivum of abdominal segment 5 less than twice as wide as connexivum of abdominal segment 4; connexivum of abdominal segment 6 rhomboidal, anterior and posterior margin roughly the same width. COLORATION (Figs 19A,B,D): body overall usually peach-colored or sepia tone with brown markings; anterior pronotal lobe usually with brown marking; forefemur pale, never darkened, sometimes pinkish; corium with a conspicuous tan or peach-colored transverse band. Female: Small to medium, total length: ~7.74–8.84 mm, width across lateral angles of pronotum: ~2.77–3.19 mm. COLORATION (Figs 19A,B,C,E): similar to that of males, but with less strongly contrasting markings; body predominantly peach-colored.

Biology: Specimens have been found on species of Asteraceae.

Distribution: *Phymata stanfordi* is found in the coastal mountain ranges of central and northern California as well as in the Sacramento Valley.

Discussion: We elevate *P. stanfordi* to species rank based on its unique morphology (color included) and clear molecular divergence from *P. pacifica* (see Masonick and Weirauch, 2020). These two taxa are sympatric and

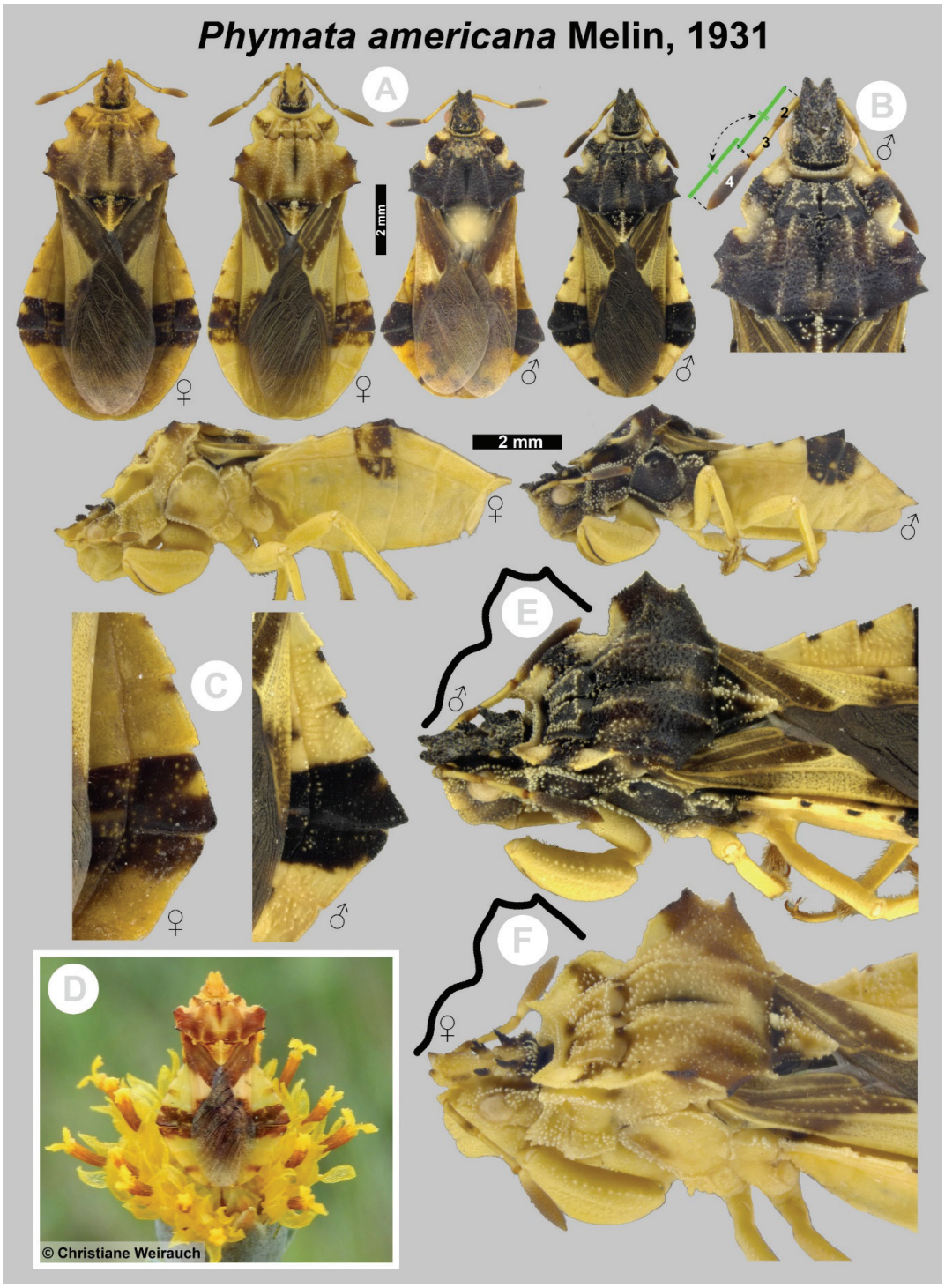
found on similar host plants. While sequence data and geometric morphometrics of pronotal shape have thus far failed to clearly separate *P. stanfordi* and *P. metcalfi* (Masonick and Weirauch, 2020), we consider both to be good species based on morphological traits (particularly granulation and color) and their geographic distributions.

Identification remarks: *Phymata stanfordi* is overall very similar to *P. metcalfi*, but can be separated using a combination of these characteristics: (1) *P. stanfordi* with distinctive peach or beige body coloration and with extensive fine granulation, (2) area between lateral pronotal notch and longitudinal carina of the posterior pronotal lobe usually with diffuse granulation (never with a dense cluster like *P. pacifica*, but with more granulation than *P. metcalfi*), (3) carina of the lateral angle lined with granulation (compare with *P. metcalfi* where granulation is usually absent), and (4) basal spot on connexiva of abdominal segments 3 and 4 usually absent. The geographic distribution of *P. stanfordi* is also much smaller than that of *P. metcalfi*.

Type information: Only paratypes of *P. pacifica stanfordi* were examined. Evans deposited the holotype in the collection at Stanford University, however we were unable to locate it there or in two neighboring institutions (the California Academy of Sciences and the Essig Museum of Entomology at the University of California, Berkeley).

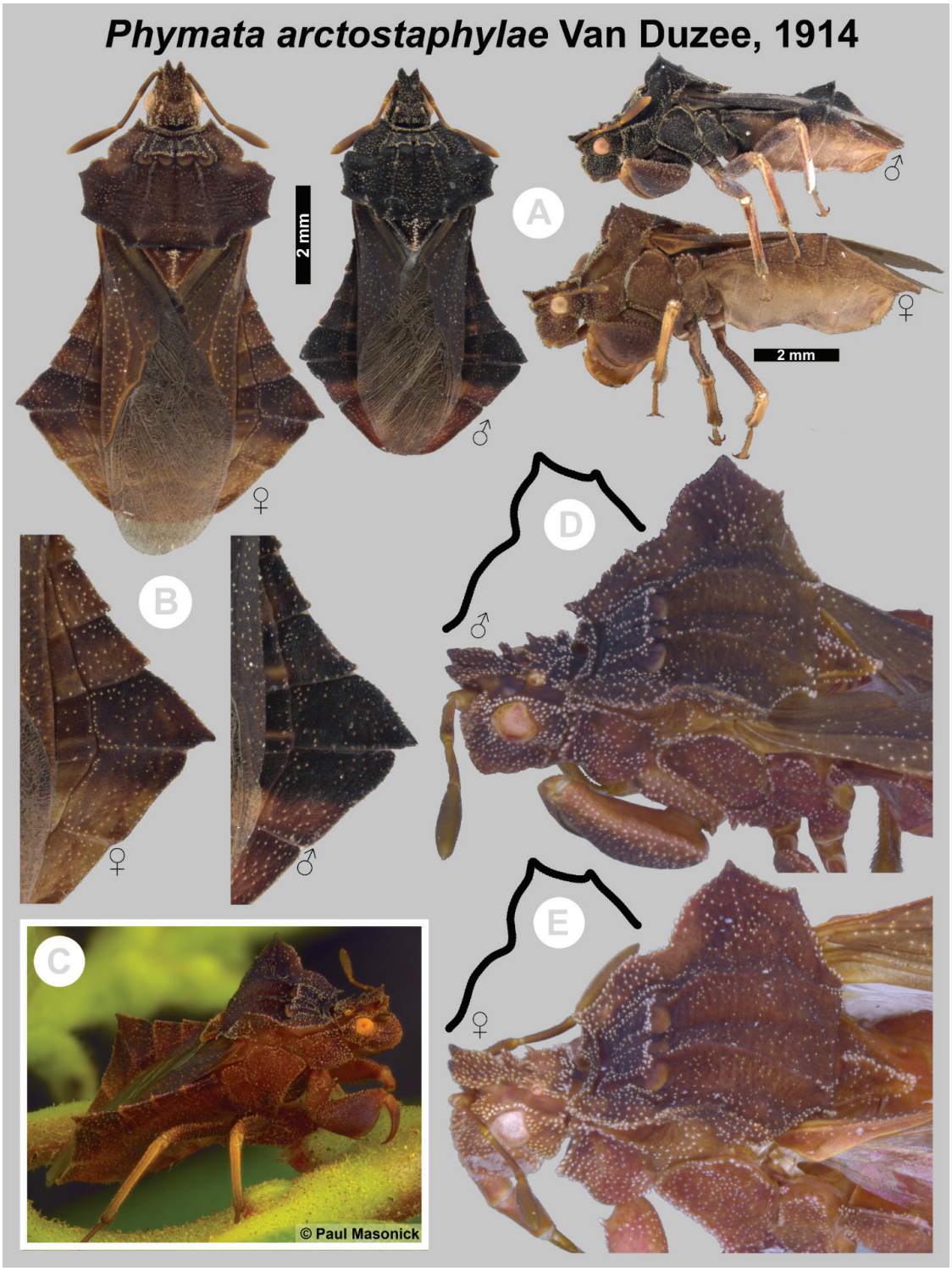
PARATYPES: **USA: California: *Santa Clara Co.:*** Stanford University, 37.42722°N, 122.16917°W, 04 Aug 1928, Carl D. Duncan, 1♂ (UCR_ENT 00096030), 1♀ (UCR_ENT 00096053) (LACM); Jun 1920, Unknown, 1♀ (UCR_ENT 00096054) (LACM); Sep 1897, Johnson, 1♀ (UCR_ENT 00096055) (LACM); Sep 1929, T. Zschokke, 3♀ (UCR_ENT 00096056-UCR_ENT 00096058) (LACM).

Additional material examined: See Appendix; 101 specimens examined, including 63 adult males and 37 adult females.

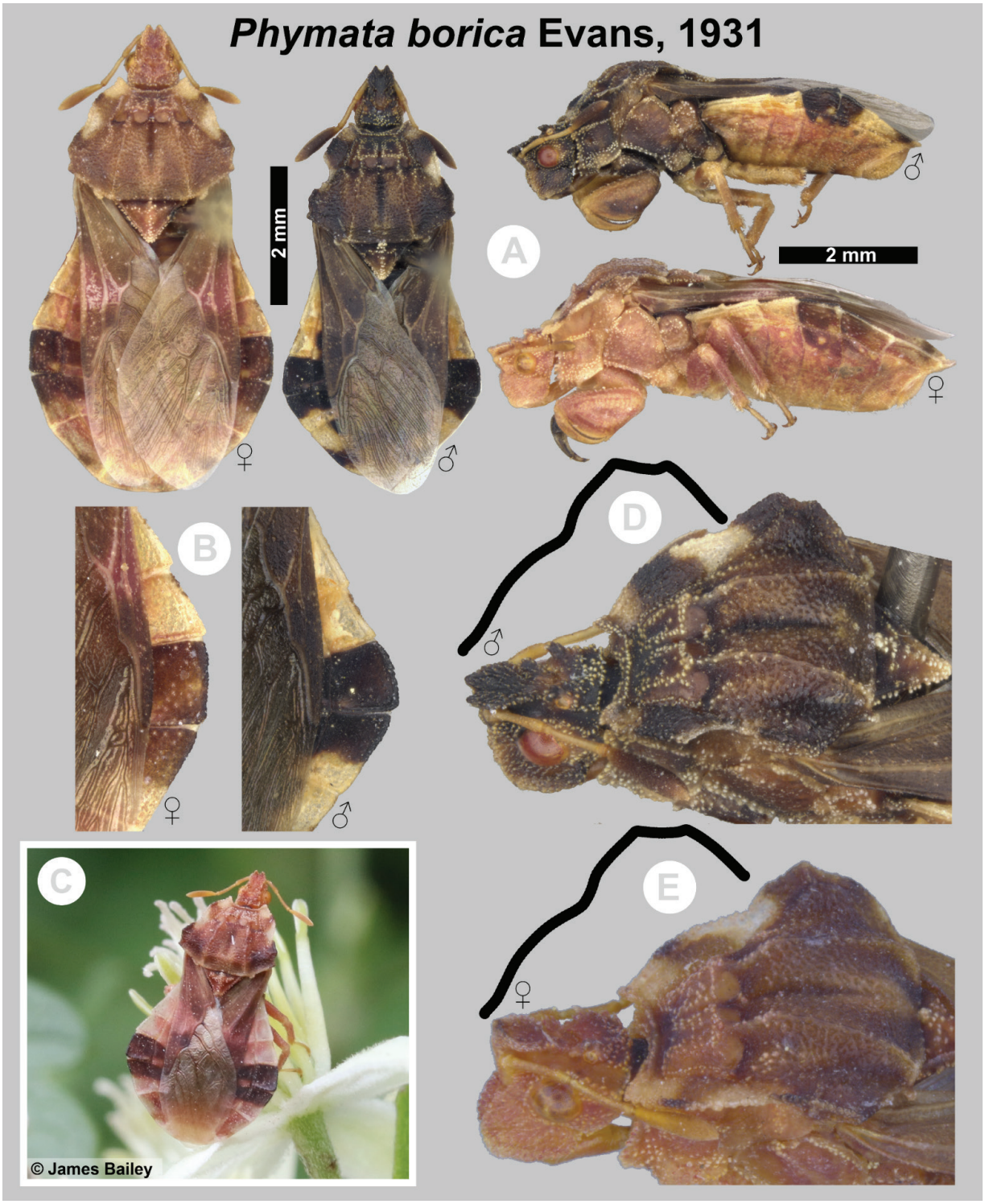


Figures 3A–F. *Phymata americana* Melin, 1931.

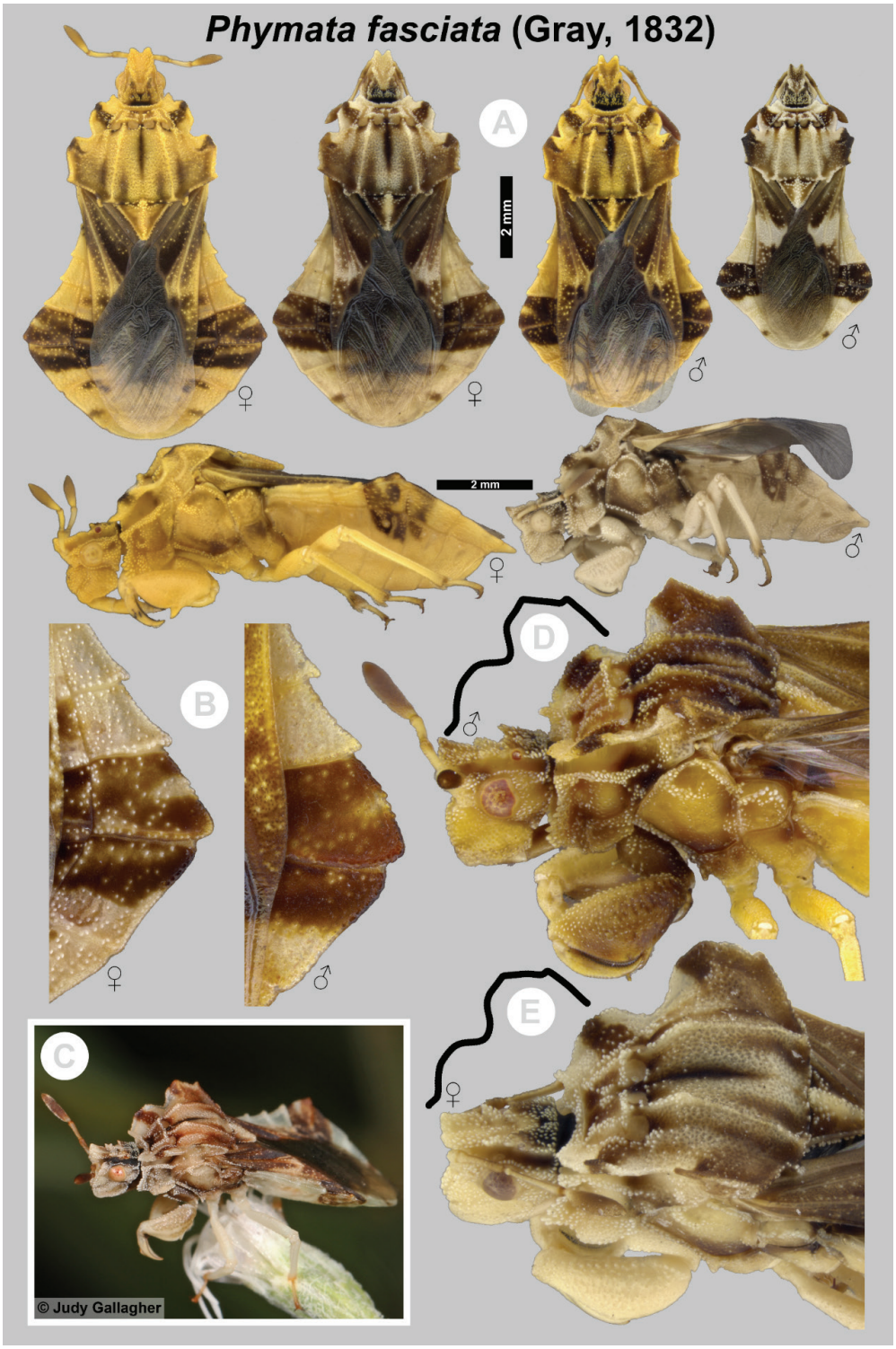
(A) Dorsal and lateral habitus images of females and males, (B) relative lengths of antennal segments in males, (C) connexival margins of female and male, (D) live female, (E) pronotal shape of males, and (F) pronotal shape of females.



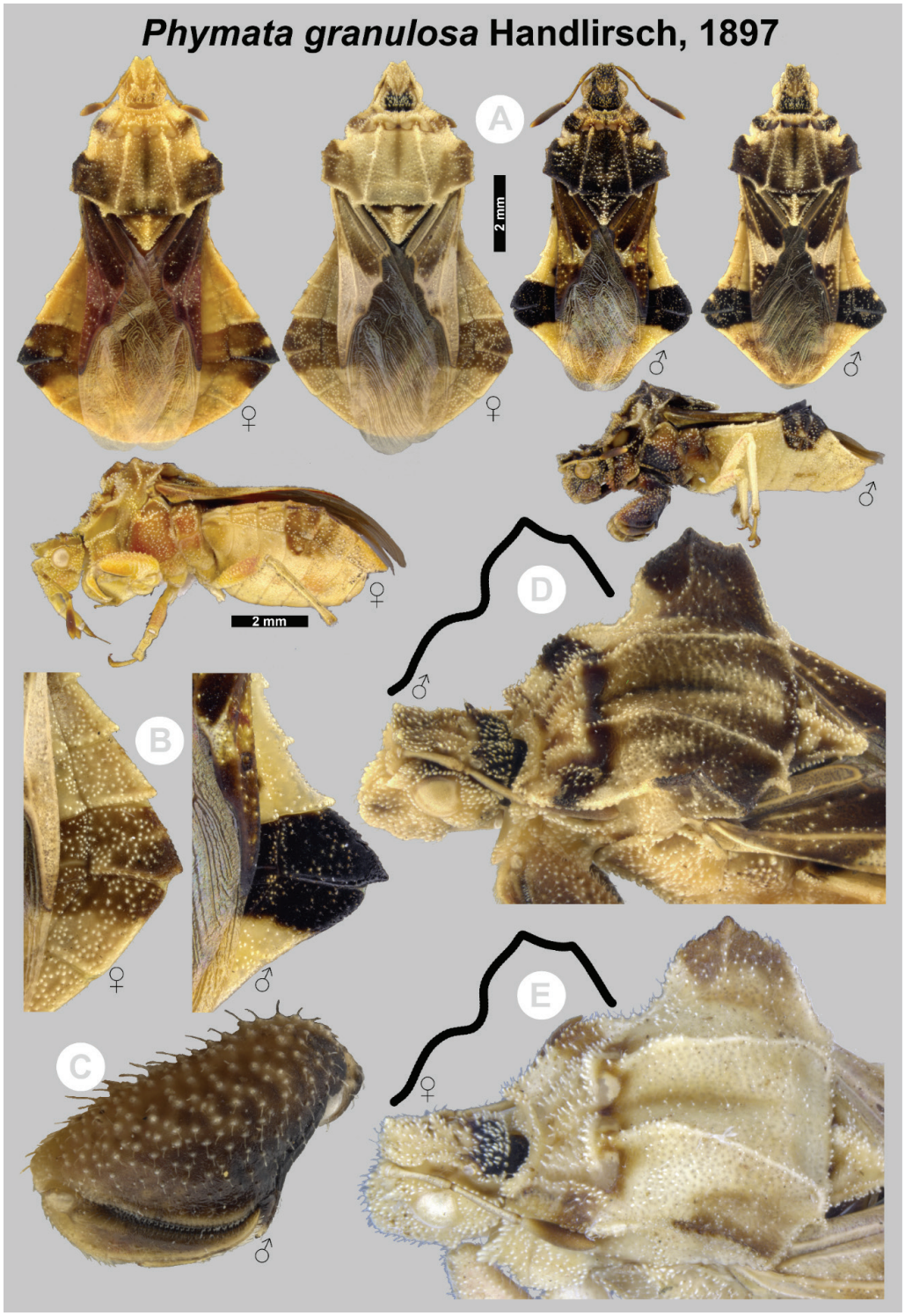
Figs 4A–E. *Phymata arctostaphylae* Van Duzee, 1914.
(A) Dorsal and lateral habitus images of female and male, (B) connexival margins of female and male, (C) live female, (D) pronotal shape of males, and (E) pronotal shape of females.



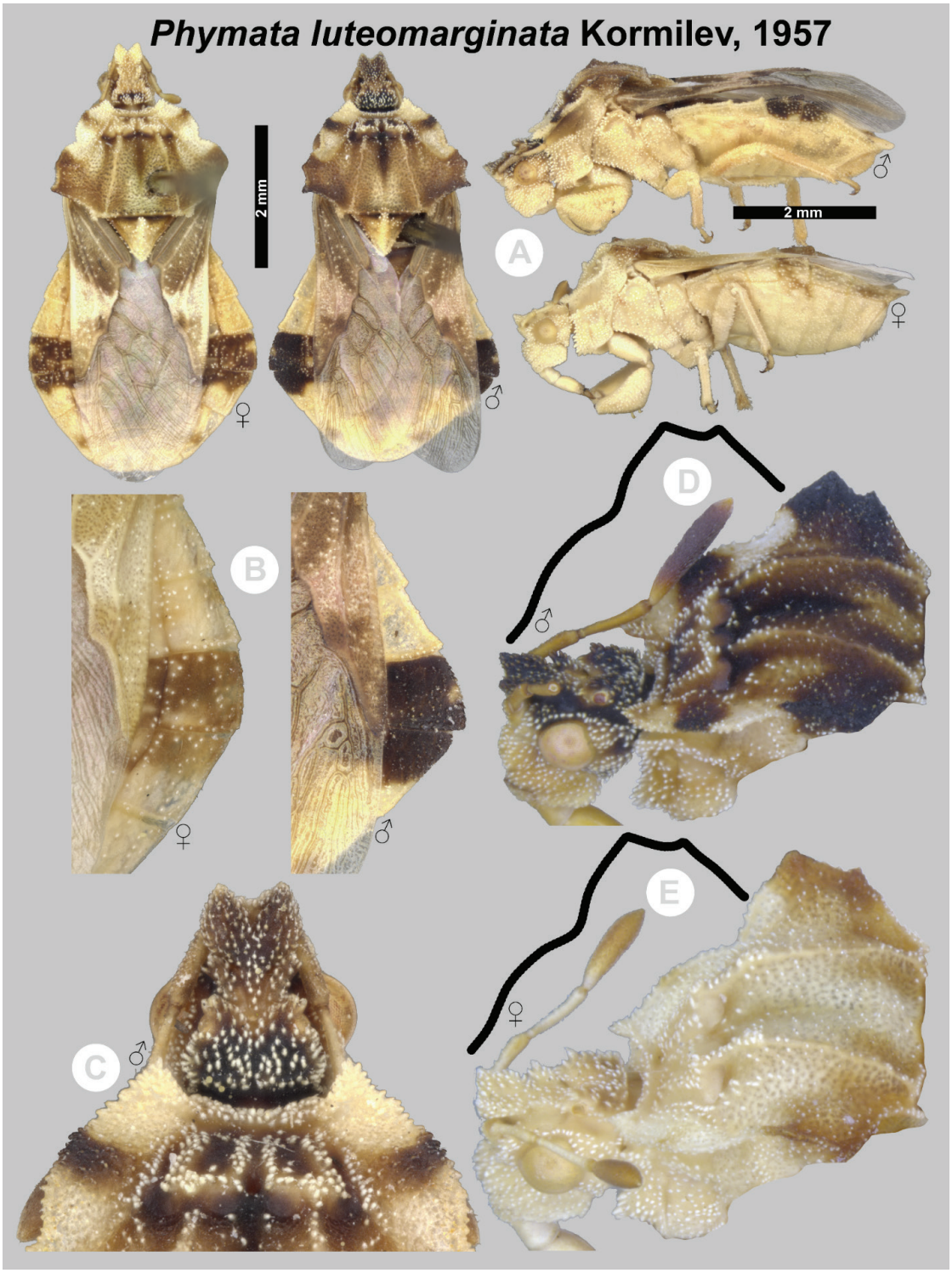
Figures 5A–E. *Phymata borica* Evans, 1931.
(A) Dorsal and lateral habitus images of female and male, (B) connexival margins of female and male, (C) live female, (D) pronotal shape of males, and (E) pronotal shape of females.



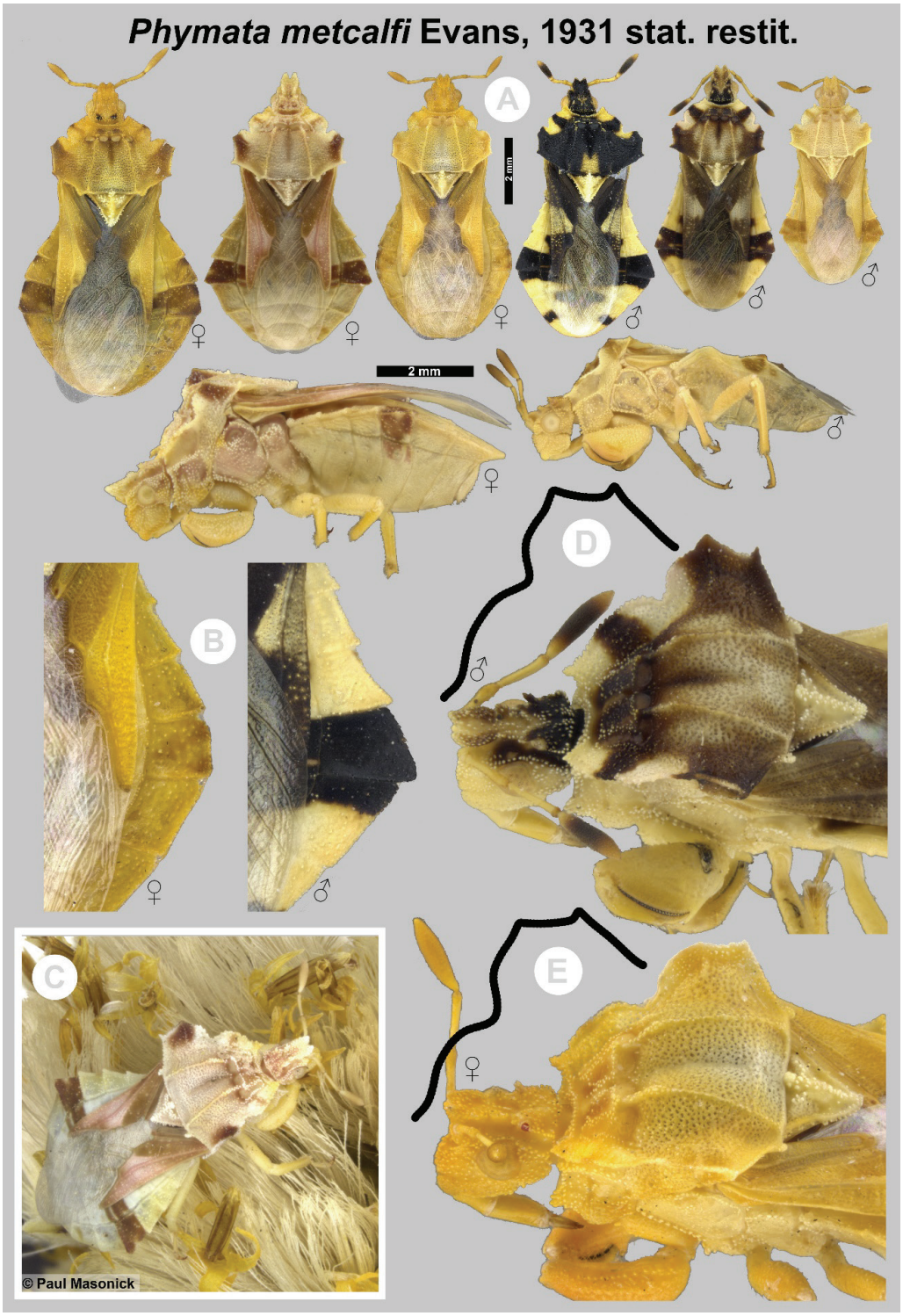
Figures 6A–E. *Phymata fasciata* (Gray, 1832).
(A) Dorsal and lateral habitus images of females and males, (B) connexival margins of female and male, (C) live male, (D) pronotal shape of males, and (E) pronotal shape of females.



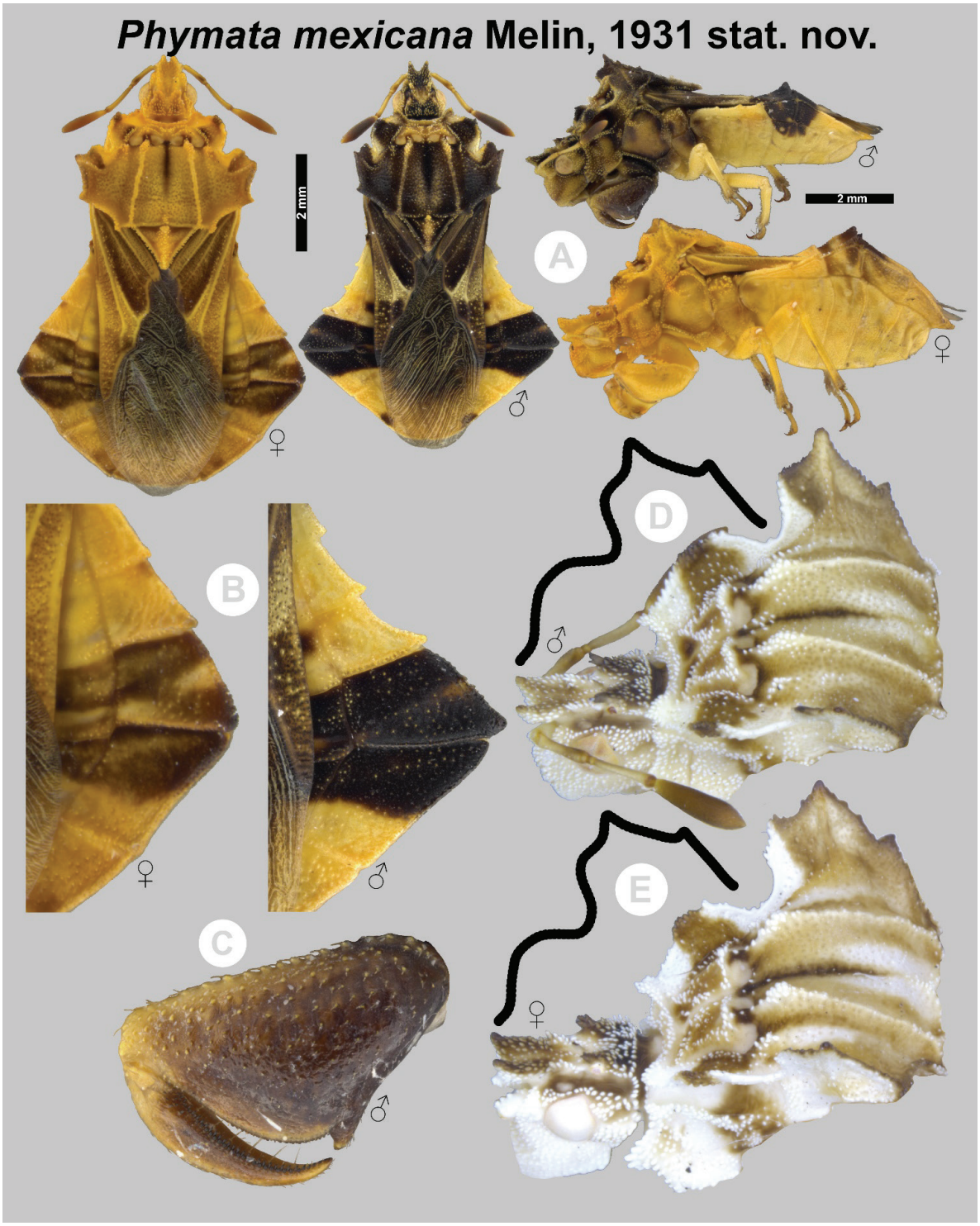
Figures 7A–E. *Phymata granulosa* Handlirsch, 1897.
(A) Dorsal and lateral habitus images of females and males, (B) connexival margins of female and male, (C) forefemur of male, (D) pronotal shape of males, and (E) pronotal shape of females.



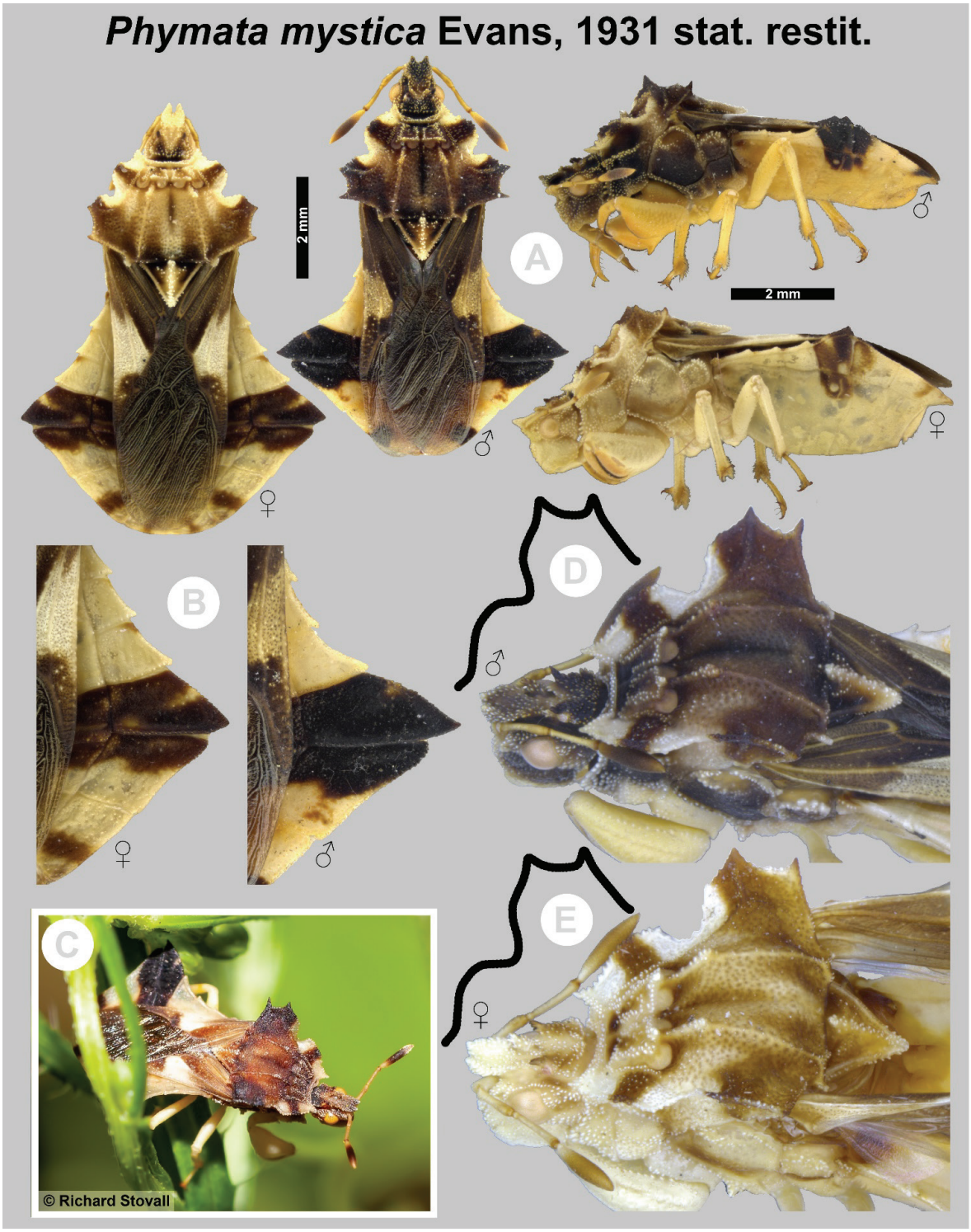
Figures 8A–E. *Phymata luteomarginata* Kormilev, 1957.
(A) Dorsal and lateral habitus images of females and males, (B) connexival margins of female and male, (C) head and anterior pronotal lobe of male, (D) pronotal shape of males, and (E) pronotal shape of females.



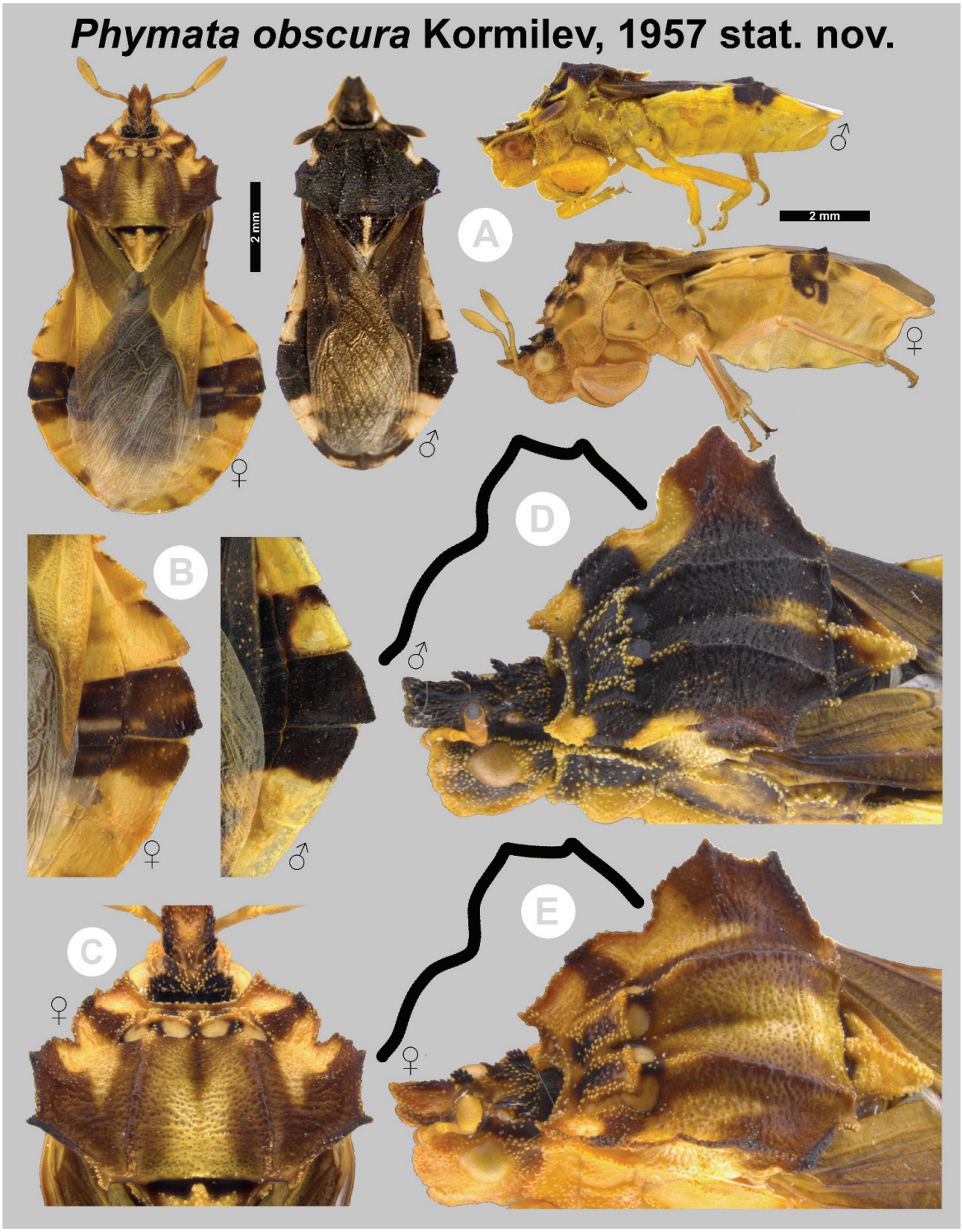
Figures 9A–E. *Phymata metcalfi* Evans, 1931 stat. restit.
(A) Dorsal and lateral habitus images of females and males, (B) connexival margins of female and male, (C) live female, (D) pronotal shape of males, and (E) pronotal shape of females.



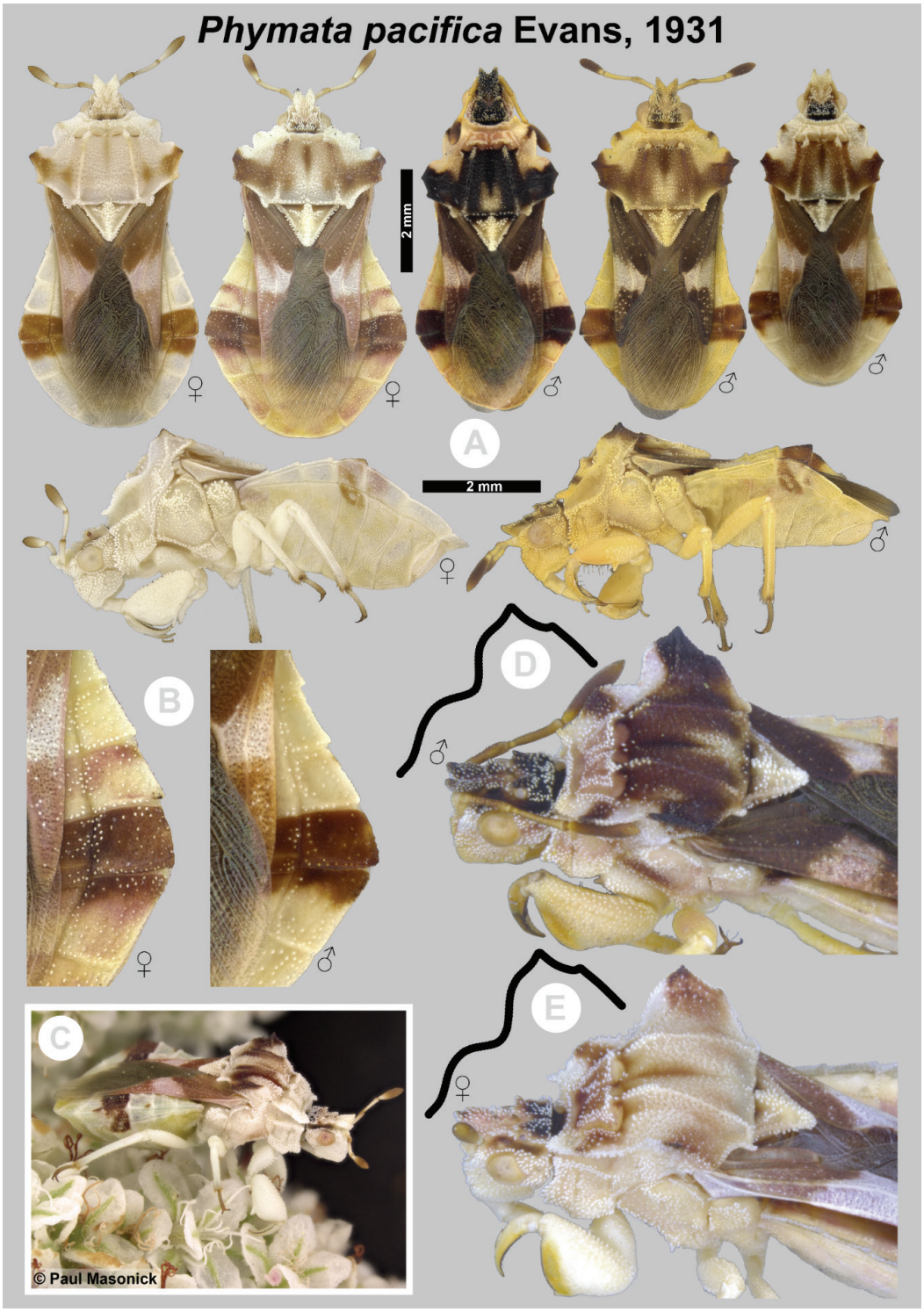
Figures 10A–E. *Phymata* mexicana Melin, 1931 stat. nov.
(A) Dorsal and lateral habitus images of female and male, (B) connexival margins of female and male, (C) forefemur of male, (D) pronotal shape of males, and (E) pronotal shape of females.



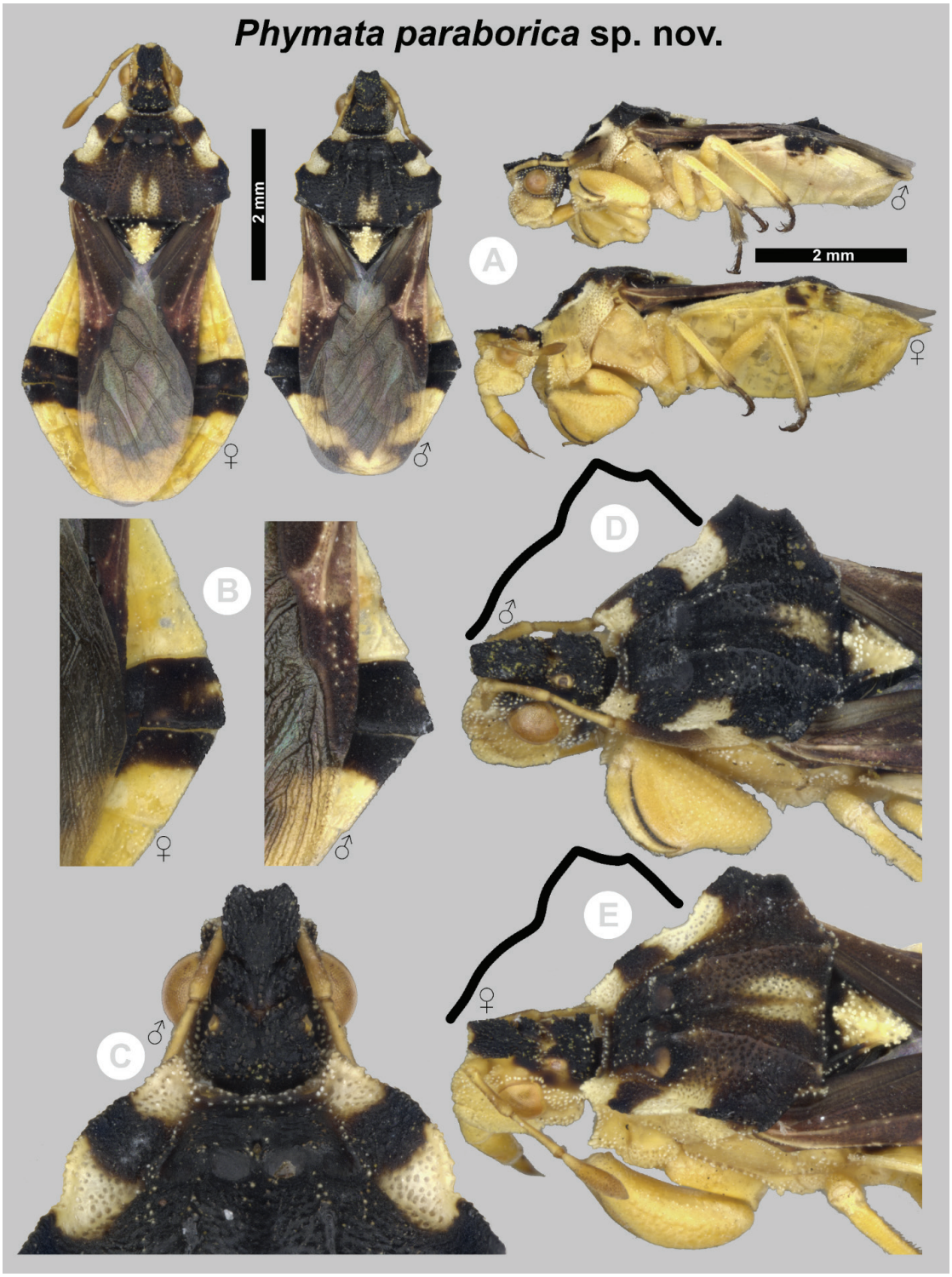
Figures 11A–E. *Phymata mystica* Evans, 1931 stat. restit.
(A) Dorsal and lateral habitus images of female and male, (B) connexival margins of female and male, (C) live male, (D) pronotal shape of males, and (E) pronotal shape of females.



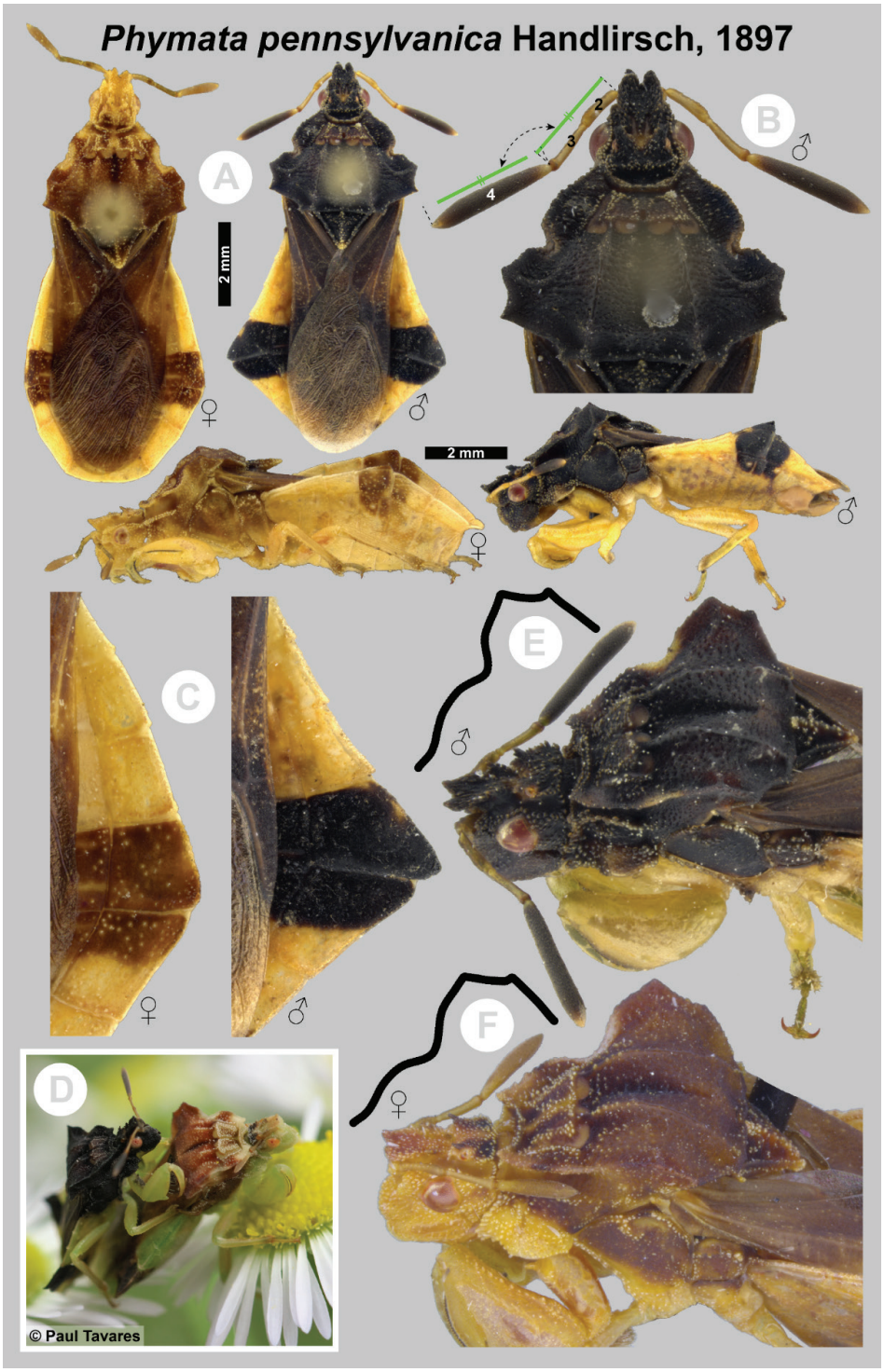
Figures 12A–E. *Phymata obscura* Kormilev, 1957 stat. nov.
(A) Dorsal and lateral habitus images of female and male Holotype, (B) connexival margins of female and male, (C) pronotum of female, (D) pronotal shape of males, and (E) pronotal shape of females.



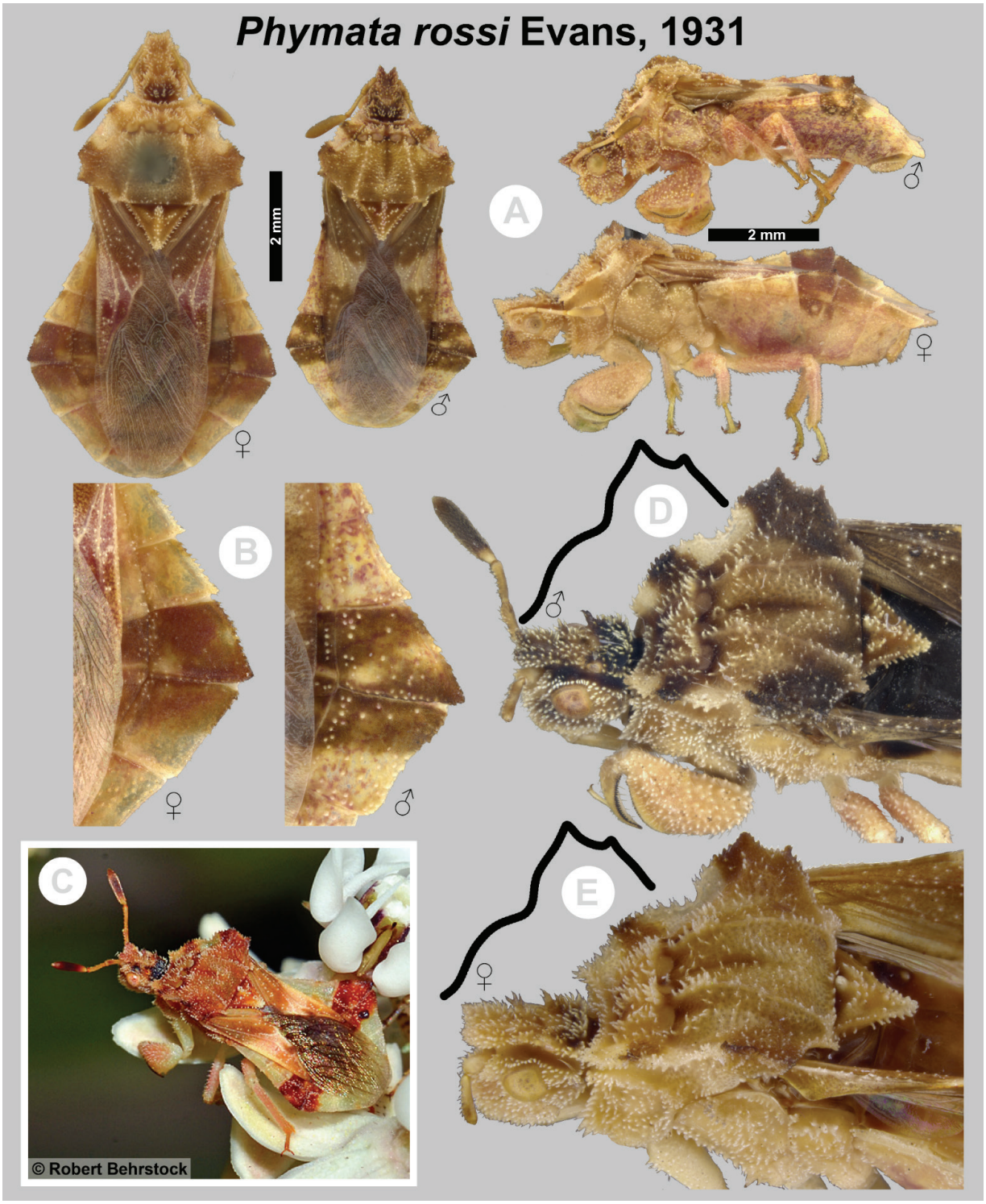
Figures 13A–E. *Phymata pacifica* Evans, 1931.
(A) Dorsal and lateral habitus images of females and males, (B) connexival margins of female and male, (C) live female, (D) pronotal shape of males, and (E) pronotal shape of females.



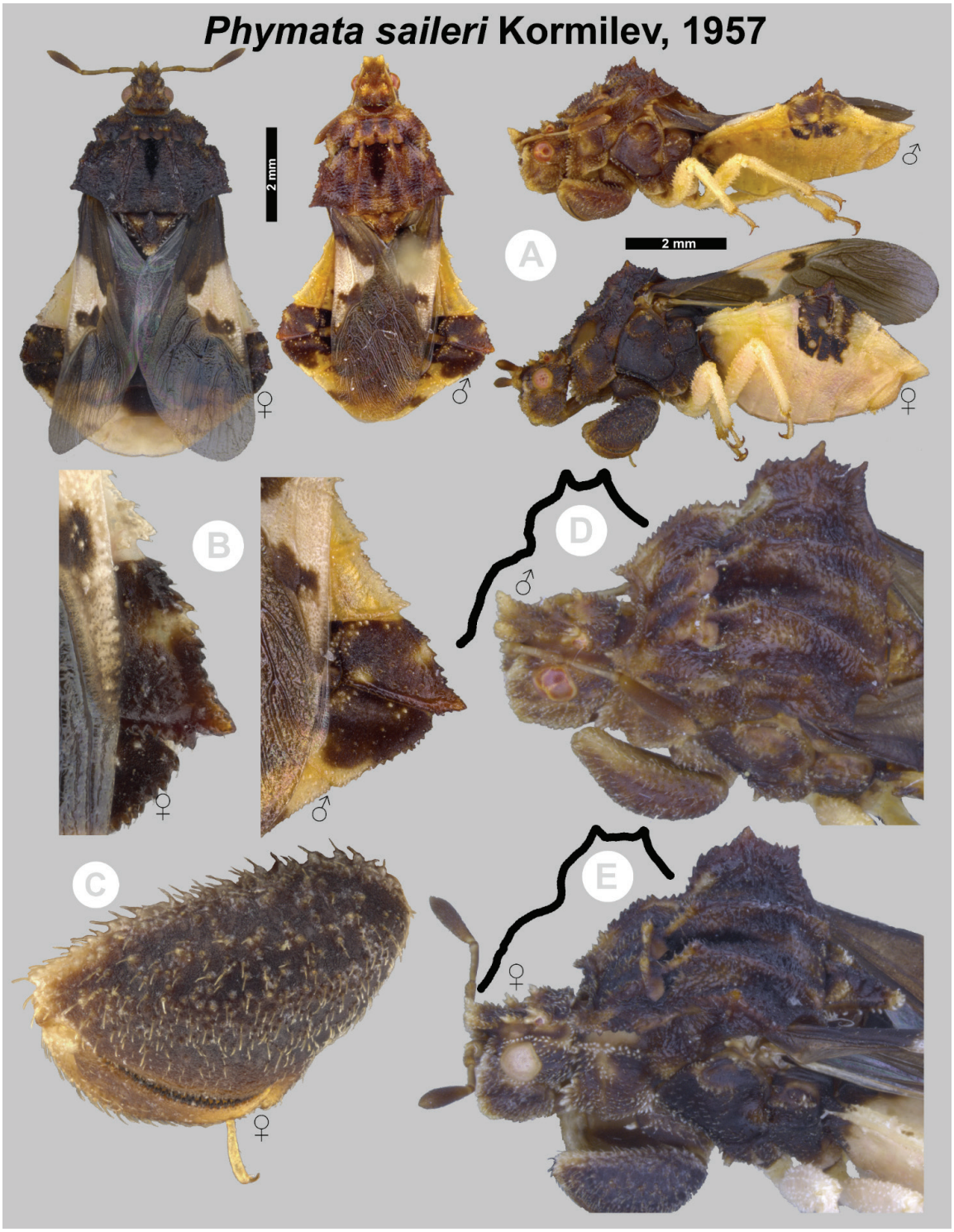
Figures 14A–E. *Phymata paraborica* sp. nov. male holotype and female allotype.
(A) Dorsal and lateral habitus images of female and male, (B) connexival margins of female and male, (C) head and anterior pronotal lobe of a male paratype, (D) pronotal shape of males, and (E) pronotal shape of females.



Figures 15A–E. *Phymata pennsylvanica* Handlirsch, 1897.
(A) Dorsal and lateral habitus images of female and male, (B) relative lengths of antennal segments in males (C) connexival margins of female and male, (D) male mate guarding female, (E) pronotal shape of males, and (F) pronotal shape of females.



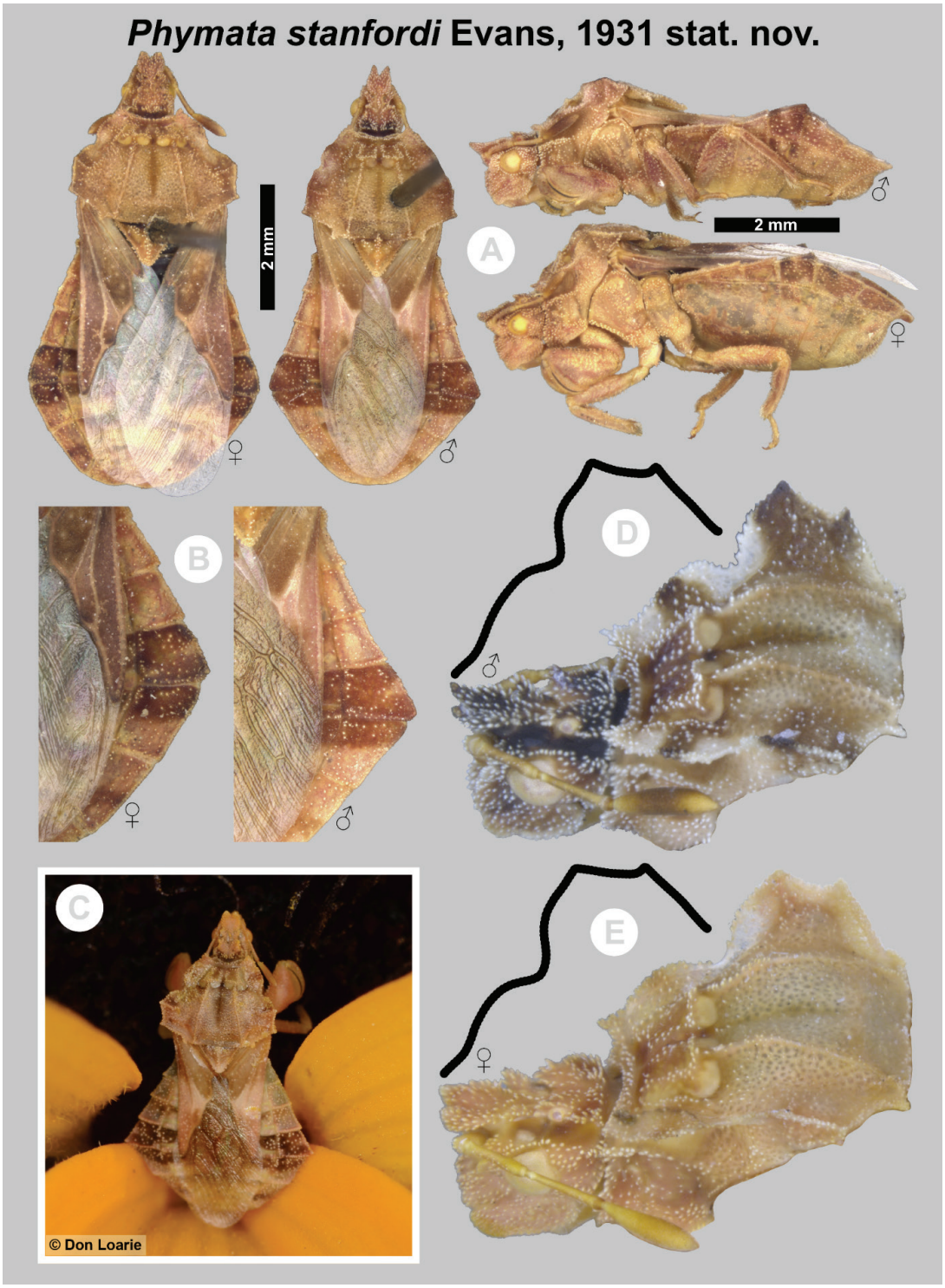
Figures 16A–E. *Phymata rossi* Evans, 1931.
(A) Dorsal and lateral habitus images of female and male, (B) connexival margins of female and male, (C) live male on Arizona milkweed (Asclepias angustifolia Schweigg.), (D) pronotal shape of males, and (E) pronotal shape of females.



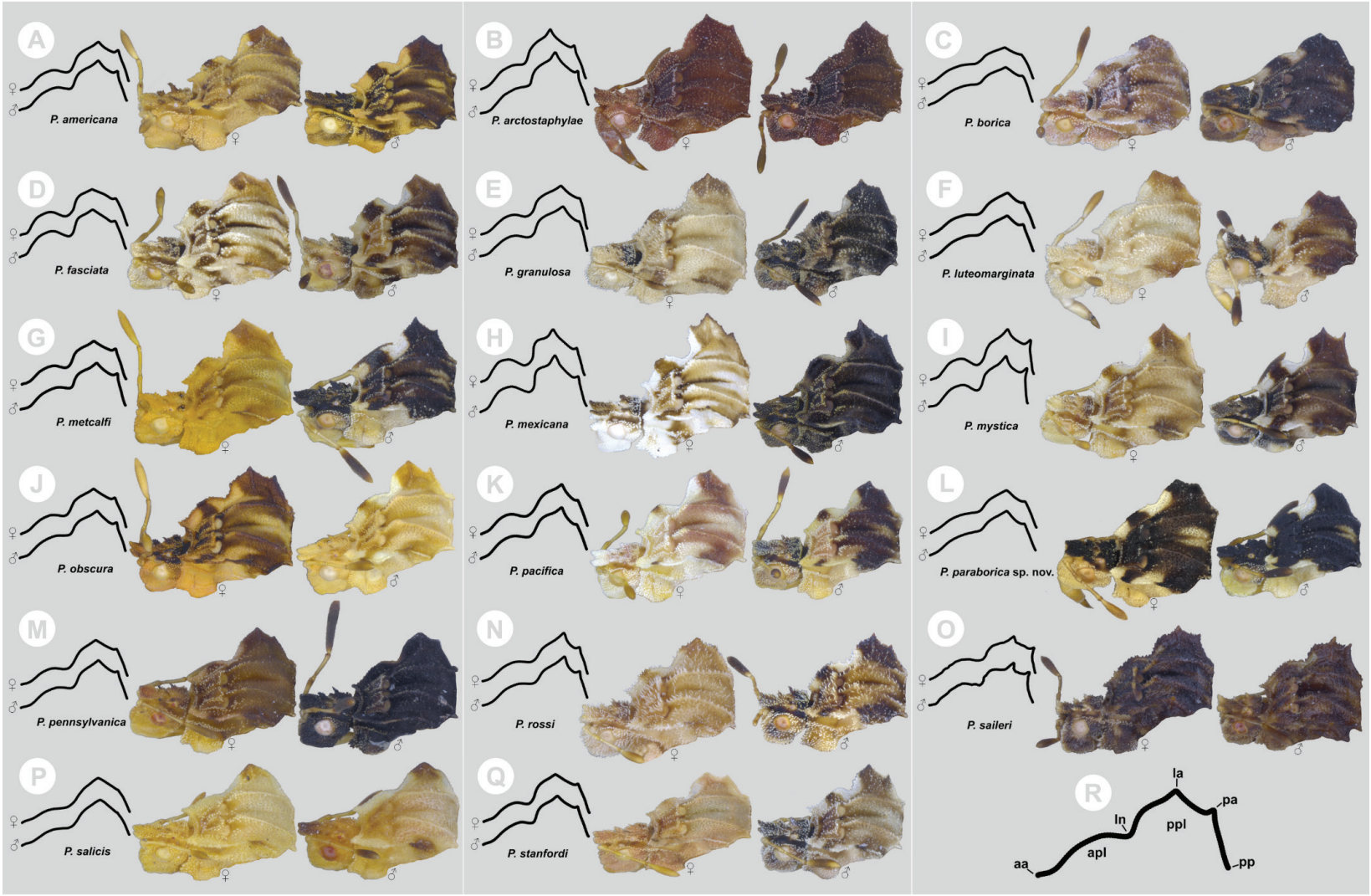
Figures 17A–E. *Phymata saileri* Kormilev, 1957.

(A) Dorsal and lateral habitus images of female and male, (B) connexival margins of female and male, (C) forefemur of female, (D) pronotal shape of males, and (E) pronotal shape of females.

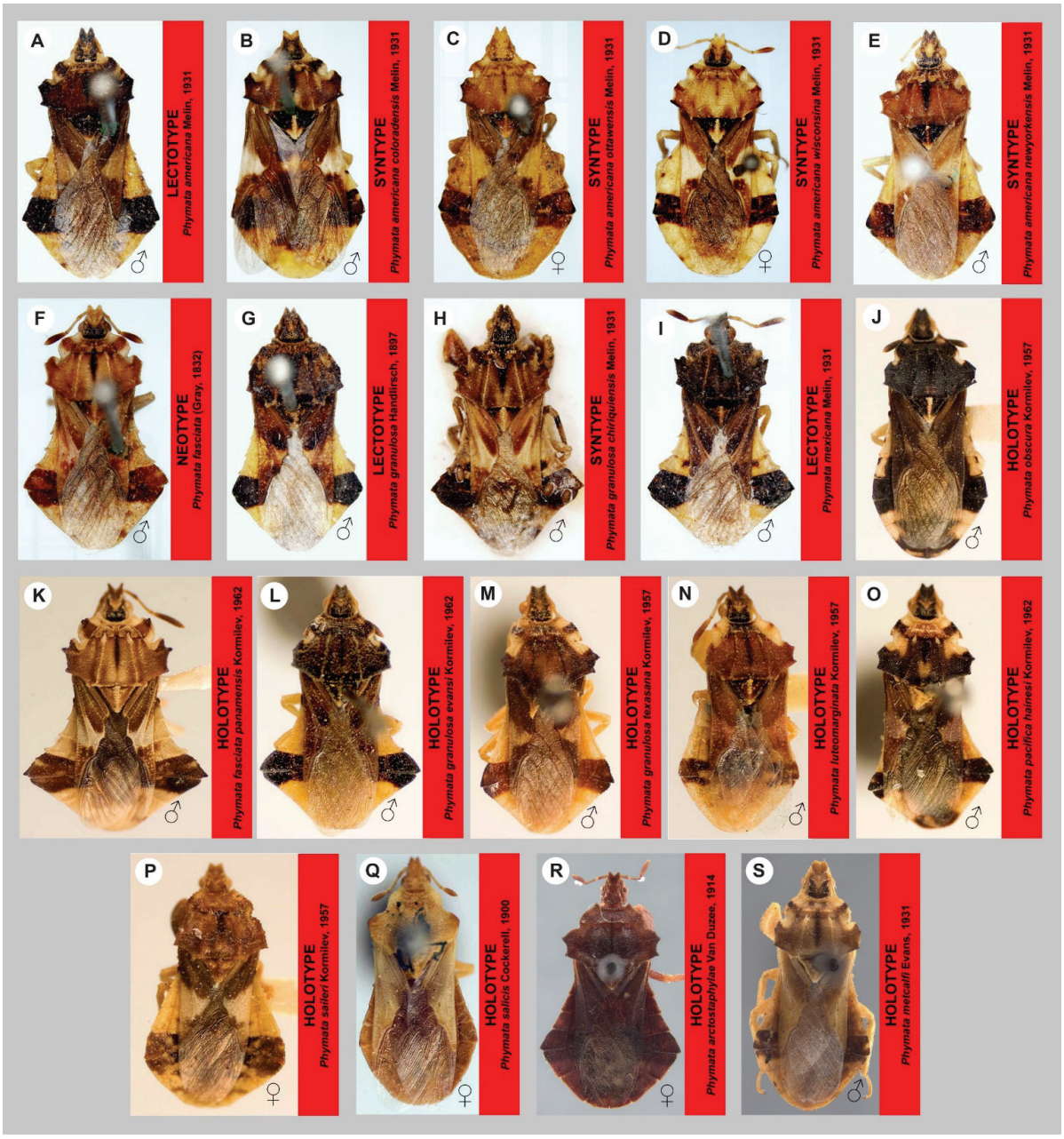
Figures 18A–D. *Phymata salicis* Cockerell, 1900.
(A) Dorsal and lateral habitus images of female and males, (B) connexival margins of female and male, (C) pronotal shape of males, and (D) pronotal shape of females.



Figures 19A–E. *Phymata stanfordi* Evans, 1931 stat. nov.
(A) dorsal and lateral habitus images of female and male, (B) connexival margins of female and male, (C) live female, (D) pronotal shape of males, and (E) pronotal shape of females.

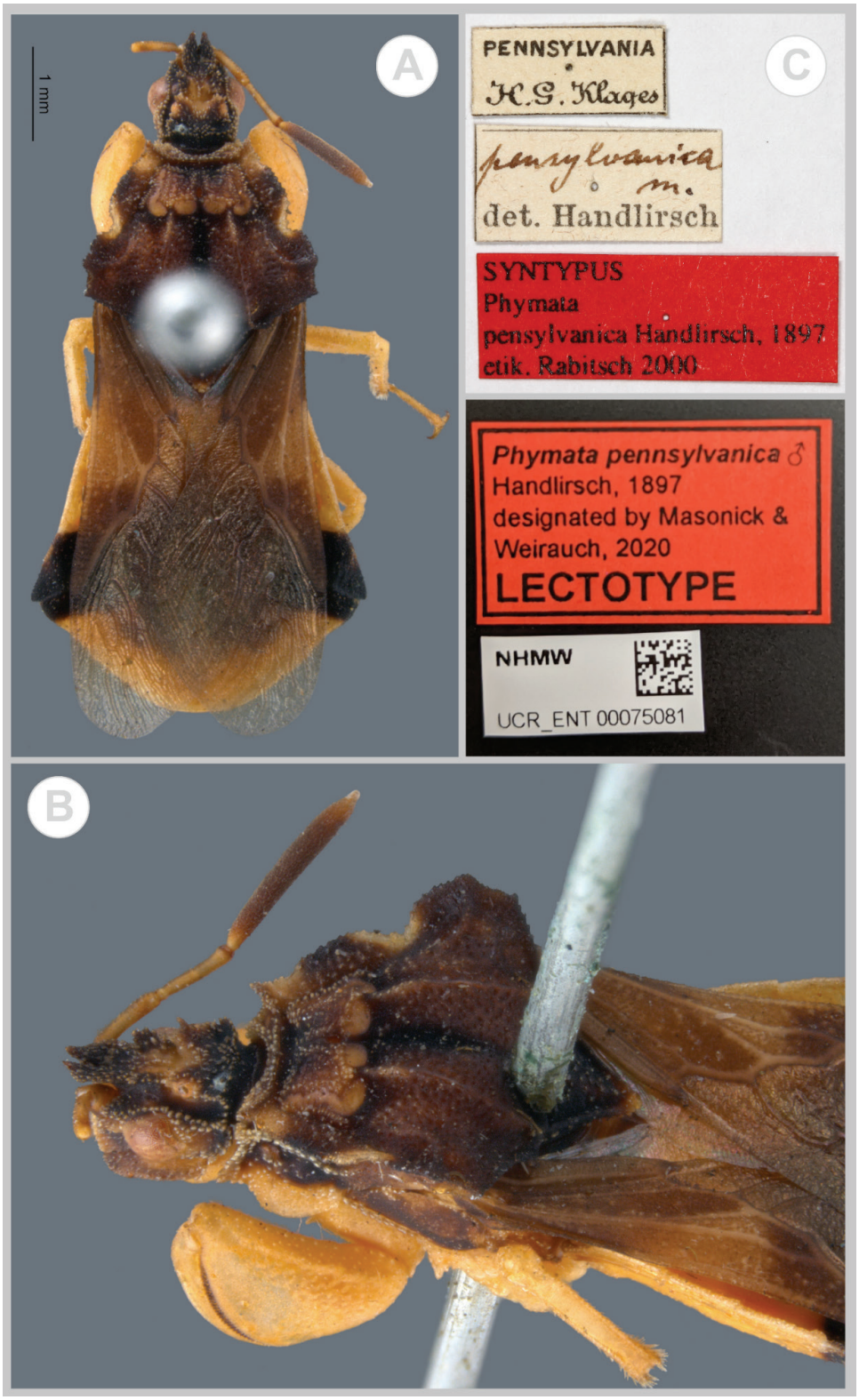


Figures 20A–R. Pronotal shape variation across the Nearctic *erosa* species group.



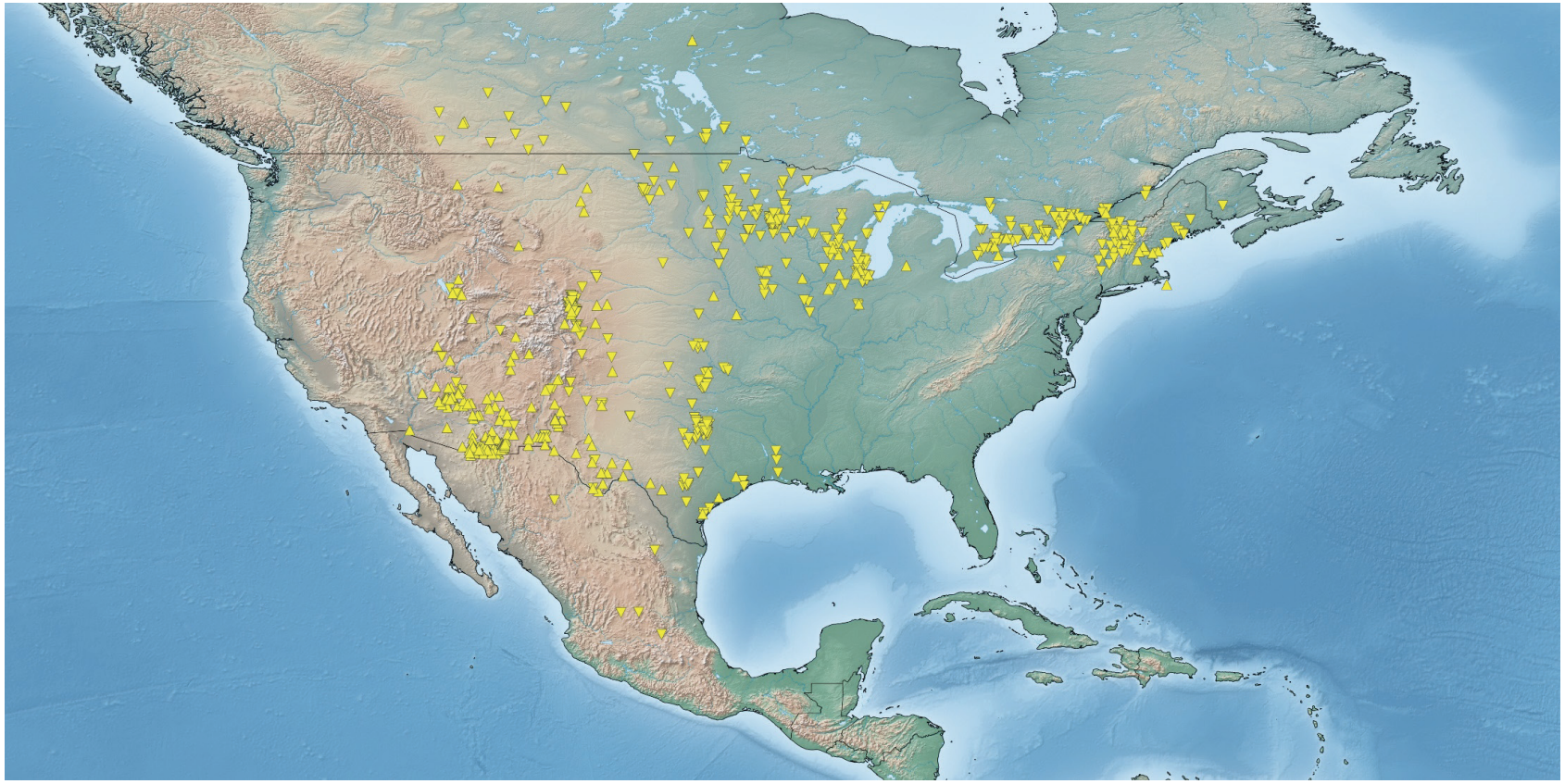
Figures 21A–S. Type specimens examined.

(A—I) Type specimens deposited in the NRM, photos © Swedish Museum of Natural History, (J—Q) type specimens deposited in the USNM, photos © United States National Museum of Natural History, and (R—S) type specimens deposited in the CAS, photos © California Academy of Sciences, photos by Rachel Diaz-Bastin.



Figures 22A–C. Lectotype herein designated for *Phymata pennsylvanica* Handlirsch, 1897.
(A) Dorsal habitus, (B) dorsolateral view of head and thorax, and (C) associated labels. © Natural History Museum Image Collection, photos by Harald Bruckner.

Phymata americana Melin, 1931



Specimens (△): 755; iNaturalist observations (▽): 663.

doi:10.3752/cjai.2020.41

Phymata arctostaphylae Van Duzee, 1914

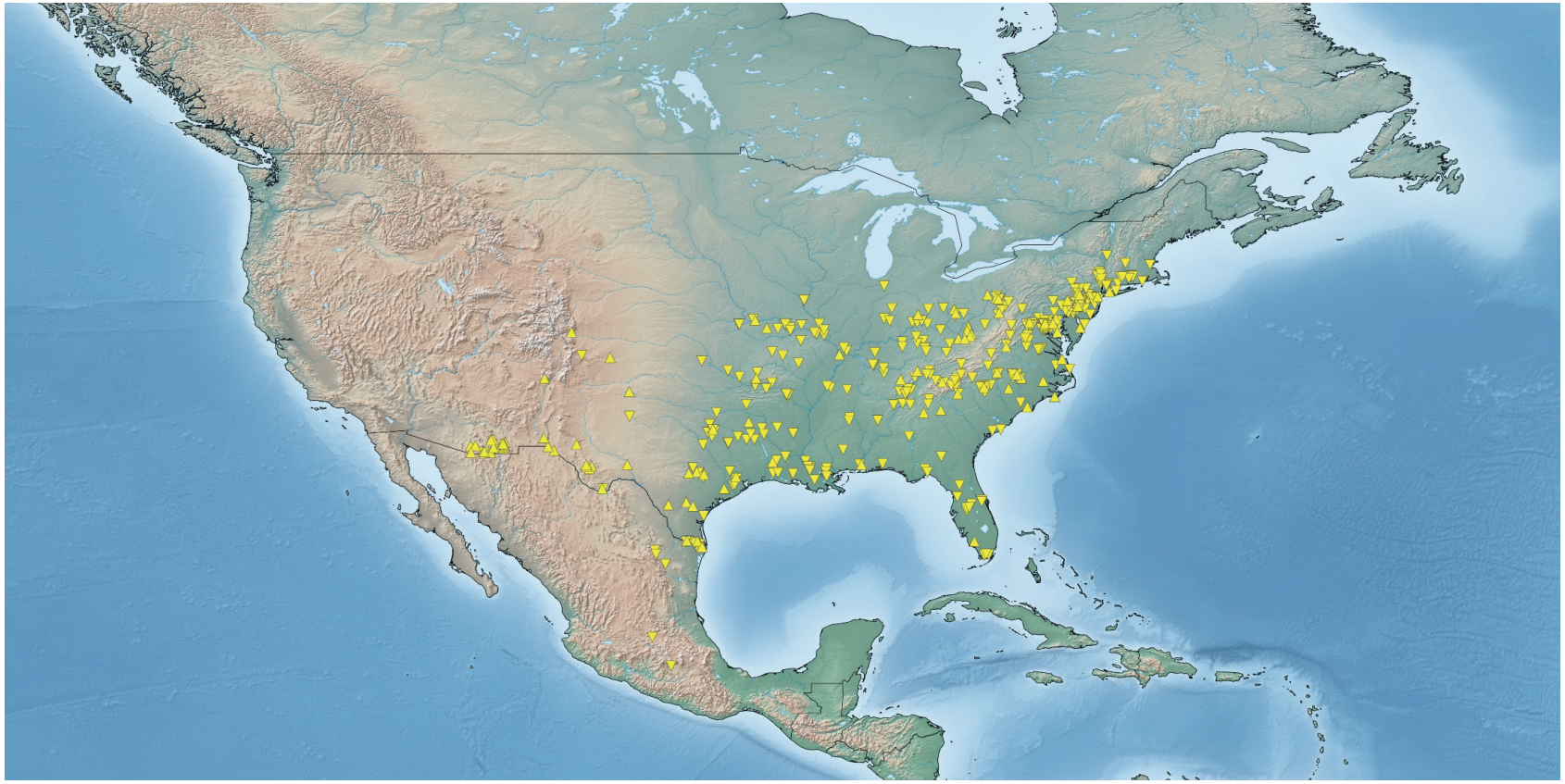
Specimens (△): 55; iNaturalist observations (▽): 0.

Phymata borica Evans, 1931

Specimens (△): 41; iNaturalist observations (▽): 7.

doi:10.3752/cjai.2020.41

Phymata fasciata (Gray, 1832)



Specimens (△): 285; iNaturalist observations (▽): 444.

doi:10.3752/cjai.2020.41

Phymata granulosa Handlirsch, 1897

Specimens (△): 44; iNaturalist observations (▽): 2.

doi:10.3752/cjai.2020.41

Phymata luteomarginata Kormilev, 1957

Specimens (△): 38; iNaturalist observations (▽): 2.

Phymata metcalfi Evans, 1931 stat. restit.

Specimens (△): 686; iNaturalist observations (▽): 49.

Phymata mexicana Melin, 1931 stat. nov.

Specimens (△): 59; iNaturalist observations (▽): 9.

Phymata mystica Evans, 1931 stat. restit.

Specimens (△): 100; iNaturalist observations (▽): 63.

Phymata obscura Kormilev, 1957 stat. nov.

Specimens (△): 180; iNaturalist observations (▽): 8.

Phymata pacifica Evans, 1931

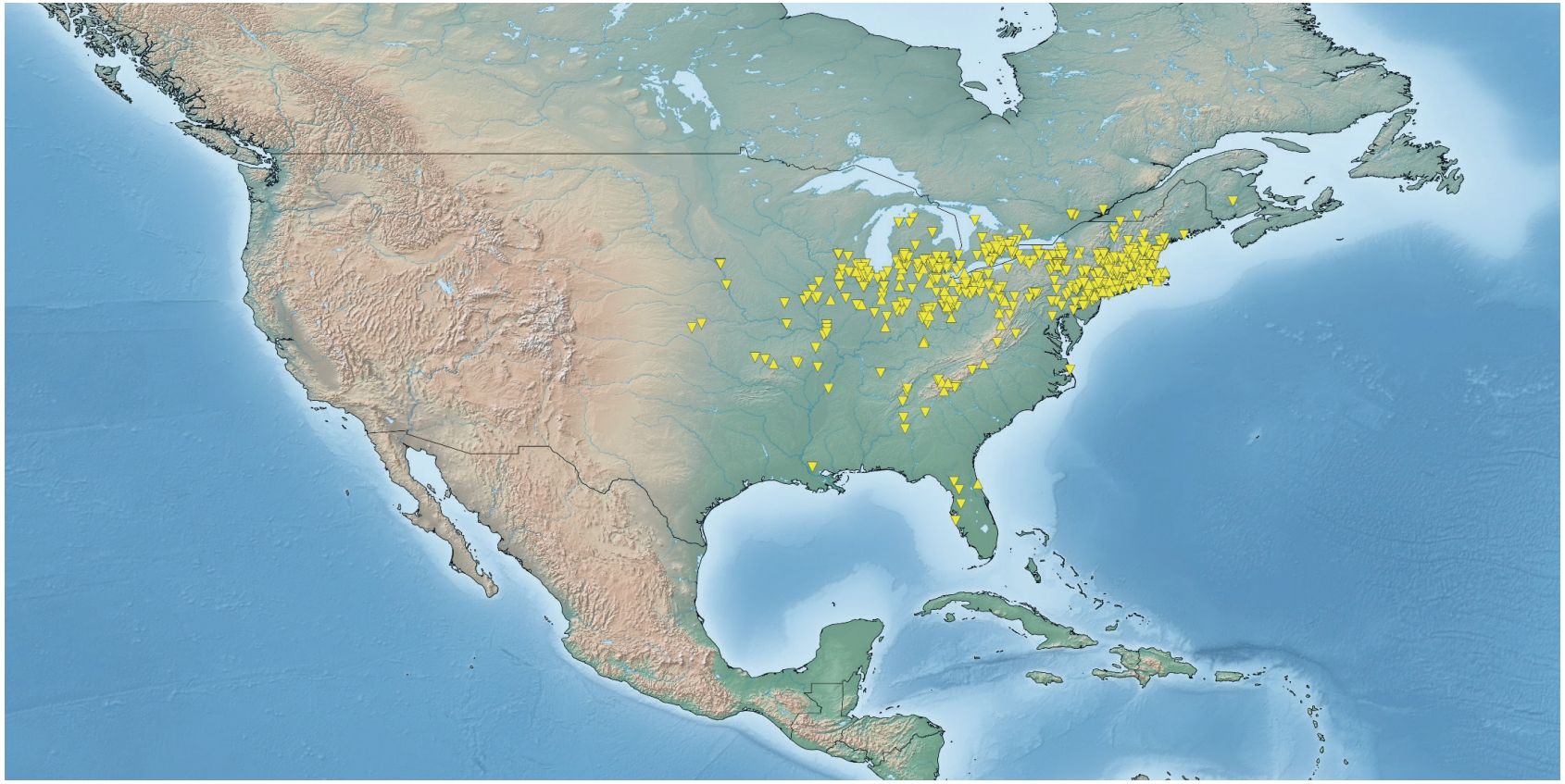
Specimens (△): 933; iNaturalist observations (▽): 82.

doi:10.3752/cjai.2020.41

Phymata paraborica sp. nov.

Specimens (△): 79; iNaturalist observations (▽): 0.

Phymata pennsylvanica Handlirsch, 1897



Specimens (△): 123; iNaturalist observations (▽): 951.

doi:10.3752/cjai.2020.41

Phymata rossi Evans, 1931

Specimens (△): 107; iNaturalist observations (▽): 2.

doi:10.3752/cjai.2020.41

Phymata saileri Kormilev, 1957

Specimens (△): 4; iNaturalist observations (▽): 0.

doi:10.3752/cjai.2020.41

Phymata salicis Cockerell, 1900

Specimens (△): 23; iNaturalist observations (▽): 0.

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Phymata stanfordi Evans, 1931 stat. nov.

Specimens (△): 108; iNaturalist observations (▽): 8.

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