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Aspects of the Biogeography of North American Psocoptera (Insecta)

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1. Introduction

The group under consideration here is the classic order Psocoptera as defined in the Torre-Bueno Glossary of Entomology (Nichols & Shuh, 1989). Although this group is unquestionably paraphyletic (see Lyal, 1985, Yoshizawa & Lienhard, 2010), these free-living, non-ectoparasitic forms are readily recognizable.

In defining North America for this chapter, I adhere closely to Shelford (1963, Fig. 1-9), but I shall use the Tropic of Cancer as the southern cut-off line, and I exclude the Antillean islands. Although the ranges of many species of Psocoptera extend across the Tropic of Cancer, the inclusion of the tropical areas would involve the comparison of relatively well-studied regions and relatively less well-studied regions.

The North America Psocoptera, as defined above, comprises a faunal list of 397 species in 90 genera and 27 families (Table 1) . Comparisons are made here with several other relatively well-studied faunas. The psocid fauna of the Euro-Mediterranean region, summarized by Lienhard (1998) with additions by the same author (2002, 2005, 2006) and Lienhard & Baz (2004) has a fauna of 252 species in 67 genera and 25 families. As would be expected, nearly all of the families are shared between the two regions. The only two families not shared are Ptiloneuridae and Dasydemellidae, which reach North America but not the western Palearctic. Ptiloneuridae has a single species and Dasydemellidae two in North America. The rather large differences at the generic and specific levels are probably due to the much greater access that these insects have for invasion of North America from the tropics than invasion from the tropics in the Western Palearctic. In the latter region, the Sahara Desert and its eastward extension through the Middle East have severely limited northward movement from tropical sub-Saharan Africa. In North America, the copiously varied climates and topography of Mexico and the proximity of the Antillean islands to the Florida peninsula apparently have allowed numerous invasions and/or re-invasions of North America by tropical psocid taxa. Examples will be discussed below.

Suborder Trogiomorpha
    Infraorder Atropetae
        Family Lepidopsocidae
            Subfamily Echinopsocinae

Cyptophania sp. N, 2
Neolepolepis caribensis (Turner) N, 2
N. occidentalis (Mockford) N, 1
N. xerica García Aldrete N, 6
Pteroxanium forcepeta García Aldrete N, 6
P. kelloggi (Ribaga) C, 5
Subfamily Lepidopsocinae
Echmepteryx (Echmepteryx) alpha García Aldrete N, 2
E. (*E.*) *hageni* (Packard) N, 1
E. (*E.*) *intermedia* Mockford N, 2
E. (*E.*) *youngi* Mockford N, 2
E. (*Thylacopsis*) *falco* Badonnel N, 2
E. (*T.*) *madagascariensis* (Kolbe) N, 2
E. (*T.*) sp. N, 2
Subfamily Perientominae
Nepticulomima sp. N, 2
Proentomum personatum Badonnel N, 2
Soa flaviterminata Enderlein N, 2
Subfamily Thylacellinae
Thylacella cubana (Banks) N, 2
Family Psoquillidae
Balliella ealensis Badonnel N, 1 (?)
Psoquilla marginepunctata Hagen IC, 2
Rhyopsocoides typhicola García Aldrete N, 6
Rhyopsocus bentonae Sommerman N, 2
R. disparilis (Pearman) I
R. eclipticus Hagen N, 1
R. maculosus García Aldrete N, 6
R. micropterus Mockford N, 5
R. texanus (Banks) N, 4, 6
R. sp. nr. *bentonae* N, 2
Family Trogiidae
Cerobasis annulata (Hagen) IC (dom)
C. guestfalica (Kolbe) N, 1, 2
C. sp. #1 N, 2
C. sp. #2 N, 1
C. sp. #3 N, 5
Lepinotus inquilinus Heyden IC (dom)
L. patruelis Pearman IC (dom)
L. reticulatus Enderlein N, 4
Myrmecodipnella aptera Enderlein N, 5
Trogium braheicola García Aldrete N, 6
T. pulsatorium (Linn.) C (dom)
Infraorder Psyllipsocetae
Family Psyllipsocidae
Dorypteryx domestica (Smithers) IC (dom)

D. pallida Aaron IC (dom)
Pseudorypteryx mexicana García Aldrete N, 4, 6
Psocathropos lachlani Ribaga IC, 2
Psyllipsocus apache Mockford N, 4
P. decoratus Mockford N, 4
P. hilli Mockford N, 4
P. huastecanus Mockford N, 6
P. hyalinus García Aldrete N, 6
P. kintpuashi Mockford N, 5
P. maculatus García Aldrete N, 4, 6
P. neoleonensis García Aldrete N, 6
P. oculatus Gurney I
P. ramburii Selys-Longchamps C (dom & caves)
P. regiomontanus Mockford N, 6
P. subterraneus Mockford N, 4

Infraorder Prionoglaridetae
Family Prionoglarididae
Speleketor flocki Gurney N, 4
S. irwini Mockford N, 4
S. pictus Mockford N, 4

Suborder Troctomorpha
Infraorder Nanopsocetae
Family Pachytroctidae
Nanopsocus oceanicus Pearman IC, 2
Pachytroctes aegyptius Enderlein 2 (dom)
P. neoleonensis Garcia Aldrete N, 6
Tapinella maculata Mockford N, 4, 6
T. olmeca Mockford N, 6
Family Sphaeropsocidae
Badonnelia titei Pearman I (dom)
Prosphaeropsocus californicus Mockford N, 5
P. pallidus Mockford N, 5
Sphaeropsocopsis argentina Badonnel I
S. castanea Mockford N, 6
Troglosphaeropsocus voylesi Mockford N, 4
Family Liposcelididae
Subfamily Embidopsocinae
Belaphotroctes alleni Mockford N, 4
B. badonneli Mockford N, 2
B. ghesquierei Badonnel N, 2
B. hermosus Mockford N, 4
B. simberloffi Mockford N, 2
Embidopsocus Group IB
E. bousemani Mockford N, 1
E. laticeps Mockford N, 2
E. mexicanus Mockford N, 6

Embidopsocus Group IIA
E. citrensis Mockford N, 2
E. thorntoni Badonnel I (dom)
Embidopsocus Group IIB
E. needhami (Enderlein) N, 1
Embidopsocus Group III
E. femoralis Badonnel I (?), 2
Subfamily Liposcelidinae
Liposcelis, Section I
Group A, Subgroup Aa
L. brunnea Motschulsky C, 4
Group A, Subgroup Ab
L. deltachi Sommerman N, 4
L entomophila (Enderlein) C, 2
L. fusciceps Badonnel I
L. hirsutoides Mockford N, 2
L. nasus Sommerman N, 4
L. ornata Mockford N, 2
L pallens Badonnel N, 1
L. pallida Mockford N, 4
L. villosa Mockford N, 4
Group B, Subgroup Bb
L. bicolor (Banks) N, 1
L. decolor (Pearman) C (dom)
L. lacinia Sommerman N, 4
L. nigra (Banks) N, 1
L. pearmani Lienhard C (dom)
L. rufa Broadhead C, 1, 5
L. silvarum (Kolbe) N, 4
L. triocellata Mockford N, 5
Section II
Group C
L. formicaria (Hagen) N, 4
L. mendax Pearman C (dom)
L. obscura Broadhead C (dom)
Group D
L. bostrychophila Badonnel C, 4
L. corrodens Heymons C (dom)
L. paeta Pearman C (dom)
L. prenolepidis (Enderlein) C, 5
L. sp. N, 4
Infraorder Amphientometae
Family Amphientomidae
Lithoseopsis hellmani (Mockford & Gurney) N, 4, 6
L. hystrix (Mockford) N, 2
Stimulopalpus japonicus Enderlein I, 1

Syllisis sp. I, 2
Family Protroctopsocidae
Protroctopsocus enigmaticus Mockford N, 6
Suborder Psocomorpha
Infraorder Archipsocetae
Family Archipsocidae
Archipsocopsis frater (Mockford) N, 2
A. parvula (Mockford) N, 2
Archipsocus floridanus Mockford N, 2
A. gurneyi Mockford N, 2
A. nomas Gurney N, 2
A. sp. N, 2
Pararchipsocus elongatus Badonnel et al. I
Infraorder Epipsocetae
Family Cladiopsocidae
Cladiopsocus garciai Eertmoed I
Family Epipsocidae
Bertkauia crosbyana Chapman N, 1, 6
B. lepicidinaria Chapman N, 1
Epipsocus petenensis Mockford I
Mesepipsocus niger (New) I
Family Ptiloneuridae
Loneura sp. N, 4
Infraorder Caecilietae
Superfamily Asiopsocoidea
Family Asiopsocidae
Asiopsocus sonorensis Mockford & García Aldrete N, 4
Notiopsocus sp. N, 2
Pronotiopsocus sp. N, 2
Superfamily Caeciliusoidea
Family Amphipsocidae
Polypsocus corruptus Hagen N, 1, 5
Family Caeciliusidae
Subfamily Caeciliusinae
Tribe Maoripsocini
Maoripsocus africanus (Ribaga) C, 2
Tribe Coryphacini
Valenzuela caligonus Group
V. indicator (Mockford) N, 2
Valenzuela confluens Group
V. confluens (Walsh) N, 1
V. *gonostigma* (Enderlein) I
V. graminis (Mockford) N, 3
Valenzuela fasciatus Group
V. distinctus (Mockford) I

V. mexicanus (Enderlein) N, 6
V. nadleri (Mockford) N, 1
V. totonacus (Mockford) N, 4, 6
Valenzuela flavidus Group
V. atricornis (McLachlan) I
V. boreus (Mockford) N, 3
V. burmeisteri (Brauer) N, 3
V. croesus (Chapman) N, 2
V. flavidus (Stephens) N, 1, 5
V. hyperboreus (Mockford) N, 3
V. lochloosae (Mockford) N, 3
V. manteri (Sommerman) N, 1
V. maritimus (Mockford) N, 5
V. micanopi (Mockford) N, 2
V. perplexus (Chapman) N, 4
V. pinicola (Banks) N, 1
V. tamiami (Mockford) N, 2
Valenzuela posticus Group
V. posticus (Banks) N, 1
Valenzuela subflavus Group
V. incoloratus (Mockford) N, 2
V. juniperorum (Mockford) N, 2
V. subflavus (Aaron) N, 2
Stenocaecilius antillanus (Banks) N, 2
S. casarum (Badonnel) N, 2
S. insularum (Mockford) N, 2
Subfamily Paracaeciliinae
Xanthocaecilius anahuacensis Mockford N, 6
X. microphthalmus Mockford N, 6
X. quillayute (Chapman) N, 5, (1?)
X. sommermanae (Mockford) N, 1
X. sp. N, 4
Family Dasydemellidae
Dasydemella silvestrii Enderlein I
Teliapsocus conterminus (Walsh) N, 1, 5
Family Stenopsocidae
Graphopsocus cruciatus (Linn.) N(?) 1, 5
G. mexicanus Enderlein N, 6
Infraorder Homilopsocidea
Family Lachesillidae
Subfamily Eolachesillinae
Anomopsocus amabilis (Walsh) N, 1
Nanolachesilla chelata Mockford & Sullivan N, 2
N. hirundo Mockford & Sullivan N, 2
Prolachesilla mexicana Mockford & Sullivan N, 6

P. terricola Mockford & Sullivan N, 4

Subfamily Lachesillinae

Lachesilla andra Group

L. andra Sommerman N, 1

L. arnae Sommerman N, 3

L. dona Sommerman N, 3

L. kola Sommerman N, 4

L. nubilis (Aaron) N, 1

L. nubiloides García Aldrete N, 4

L. punctata (Banks) N, 4

L. texana Mockford & García Aldrete N, 1, 4, 6

Lachesilla centralis Group

L. centralis García Aldrete N, 5

L. cintalapa García Aldrete I

L. perezi García Aldrete N, 2 ,6

Lachesilla corona Group

L. albertina García Aldrete N, 3

L. corona Chapman N, 1

L. dispariforceps Mockford N, 6

L. dividiforceps García Aldrete N, 6

L. hermosa García Aldrete N, 6

L. michiliensis García Aldrete N, 4, 6

L. neoleonensis García Aldrete N, 6

L. picticeps Mockford N, 6

L. querpina García Aldrete N, 6

L. regiomontana García Aldrete N, 6

Lachesilla forcepeta Group

L. acuminiforceps García Aldrete N, 6

L. alpejia García Aldrete I

L. anna Sommerman N, 1

L. bottimeri Mockford & Gurney N, 2

L. chapmani Sommerman N, 2

L. cladiumicola García Aldrete N, 2

L. contraforcepeta Chapman N, 1

L. cuala García Aldrete N, 6

L. denticulata García Aldrete I

L. floridana García Aldrete N, 2

L. forcepeta Chapman N, 1

L. gracilis García Aldrete N, 2

L. kathrynae Mockford & Gurney N, 4

L. laciniosiforceps García Aldrete N, 6

L. major Chapman N, 1

L. penta Sommerman N, 2

L. typhicola García Aldrete N, 1

Lachesilla fuscipalpis Group

L. curvipila García Aldrete N, 6
L. fuscipalpis Badonnel I
Lachesilla patzunensis Group
L. bifurcata García Aldrete N, 6
Lachesilla pedicularia Group
L. aethiopica (Enderlein) N, 6
L. greeni Pearman I
L. huasteca Mockford N, 4, 6
L. otomi Mockford N, 2, 6
L. pacifica Chapman N, 5
L. pallida (Chapman) N, 1
L. pedicularia (Linn.) C, 1, 5
L. quercus (Kolbe) I (dom)
L. rena Sommerman N, 4, 6
L. tectorum Badonnel N, 4, 6
L. yucateca Mockford N, 2, 6
Lachesilla riegeli Group
L. riegeli Sommerman N,2
L. tropica García Aldrete N, 2
L. ultima García Aldrete N, 2
Lachesilla rufa Group
L. abiesicola García Aldrete N, 6
L. arida Chapman N, 4
L. aspera García Aldrete N, 6
L. braheicola García Aldrete N, 6
L. broadheadi García Aldrete N, 6
L. cupressicola García Aldrete N, 6
L. jeanae Sommerman N, 5
L. juniperana García Aldrete N, 6
L. nita Sommerman N, 2
L. pinicola García Aldrete N, 6
L. rufa (Walsh) N, 1
L. sommermanae García Aldrete N, 6
L. yakima Mockford & García Aldrete N, 5
Lachesilla sclera Group
L. sulcata García Aldrete N, 4, 6
Lachesilla texcocana Group
L. delta García Aldrete N, 6
L. monticola García Aldrete N, 6
L. texcocana García Aldrete N, 4, 6
Family Ectopsocidae
Ectopsocopsis cryptomeriae (Enderlein) N, 1
E. decorata Thornton & Wong I
Ectopsocus briggsi McLachlan N, 5
E. californicus (Banks) N, 1, 5

E. maindroni Badonnel N, 2
E. meridionalis Ribaga N, 1
E. petersi Smithers I, 5
E. pumilis (Banks) I
E. richardsi (Pearman) I
E. salpinx Thornton & Wong I
E. strauchi Enderlein I
E. thibaudi Badonnel N, 2
E. titschacki Jentsch I
E. vachoni Badonnel N, 4
E. vilhenai Badonnel N, 2
Family Peripsocidae
Kaestneriella fumosa (Banks) N, 4
K. tenebrosa Mockford & Sullivan N, 4
Peripsocus Group IA
P. madidus (Hagen) N, 1
P. milleri (Tillyard) I, 5
P. pauliani Badonnel I
P. subfasciatus (Rambur) N, 1, 5
Peripsocus Group IB
P. alachuae Mockford N, 2
P. alboguttatus (Dalman) N, 3
P. maculosus Mockford N, 1
P. madescens (Walsh) N, 1
P. minimus Mockford N, 1
P. potosi Mockford N, 4, 6
Peripsocus Group IIIB
P. phaeopterus (Stephens) I
Peripsocus Group IIIC
P. stagnivagus Chapman N, 1
Family Pseudocaeciliidae
Heterocaecilius sp. I
Ophiodopelma sp. I, 2
Pseudocaecilius citricola (Ashmead) N, 2
P. tahitiensis (Karny) N, 2
Family Trichopsocidae
Trichopsocus clarus (Banks) N, 5
T. dalii (McLachlan) I, 2
Family Philotarsidae
Aaroniella achrysa (Banks) N, 2
A. badonneli (Danks) N, 1
A. maculosa (Aaron) N, 1
Philotarsus arizonicus Mockford N, 4
P. californicus Mockford N, 5
P. kwakiutl Mockford N, 5

P. parviceps Roesler N, 3
P. potosinus Mockford N, 6
Family Elipsocidae
Cuneopalpus cyanops (Rostock) I, 1, 5
Elipsocus abdominalis Reuter N, 3
E. guentheri Mockford N, 4
E. hyalinus (Stephens) N, 3
E. moebiusi Tetens I, 3
E. obscurus Mockford N, 4
E. pumilis (Hagen) N, 3
E. sp. N, 3
Nepiomorpha peripsocoides Mockford N, 2
Palmicola aphrodite Mockford N, 2
P. solitaria Mockford N, 2
P. sp. #1 N, 2
P. sp. #2 N, 2
Propsocus pulchripennis (Perkins) I, 5
Reuterella helvimacula (Enderlein) N, 3
Family Mesopsocidae
Mesopsocus immunis (Stephens) I, 3
M. laticeps (Kolbe) N, 3
M. unipunctatus (Müller) N, 3
Infraorder Psocetae
Family Hemipsocidae
Hemipsocus chloroticus (Hagen) I, 2
H. pretiosus Banks N, 2
Family Myopsocidae
Lichenomima coloradensis (Banks) N, 4
L. lugens (Hagen) N, 1
L. sparsa (Hagen) N, 1
L. sp. #1 N, 2
L. sp. #2 N, 2
L. sp. #3 N, 1
L. sp. #4 N, 2
L. sp. #5 N, 2
L. sp. #6 N, 1
L. sp. #7 N, 1
L. sp. #8 N, 2
Myopsocus antillanus (Mockford) N, 2
M. eatoni McLachlan I
M. minutus (Mockford) N, 2
M. sp. I, 5
Family Psocidae
Subfamily Psocinae
Tribe Psocini

Atropsocus atratus (Aaron) N, 1
Hyalopsocus floridanus (Banks) N, 1
H. striatus (Walker) N, 1
H. sp. #1 N, 1
H. sp. #2 N, 4
Psocus crosbyi Chapman N, 5
P. leidyi Aaron N, 1
P. sp. N, 3

Tribe Ptyctini

Camelopsocus bactrianus Mockford N, 5
C. hiemalis Mockford N, 5
C. monticolus Mockford N, 4
C. similis Mockford N, 4
C. tucsonensis Mockford N, 4
C. sp. N, 4
Indiopsocus bisignatus (Banks) N, 1
I. campestris (Aaron) N, 2
I. ceterus Mockford N, 2
I. coquilletti (Banks) N, 5
I. infumatus (Banks) N, 1
I. texanus (Aaron) N, 2
I. sp. #1 N, 2
I. sp. #2 N, 2
I. sp. #3 N, 2
Loensia conspersa (Banks) N, 4
L. fasciata (Fabricius) I
L. maculosa (Banks) N, 5
L. moesta (Hagen) N, 1
L. sp. #1 N, 2
L. sp. #2 N, 2, 4
Ptycta lineata Mockford N, 2
P. polluta (Walsh) N, 1
Steleops elegans (Banks) N, 1
S. lichenatus (Walsh) N, 1
Trichadenotecnum alexanderae Group
- *T. alexanderae* Sommerman N, 1
- *T. castum* Betz N, 1
- *T. innuptum* Betz N, 3
- *T. merum* Betz N, 1

Trichadenotecnum circularoides Group
- *T. circularoides* Badonnel N, 2

Trichadenotecnum desolatum Group
- *T. acutilingum* Yoshizawa et al. N, 6
- *T. desolatum* (Chapman) N, 4, 6

Trichadenotecnum quaesitum Group

T. cerrosillae Yoshizawa et al. N, 6
T. maculatum Yoshizawa et al. N, 6
T. neoleonense Yoshizawa et al. N, 6
T. quaesitum (Chapman) N, 1
Trichadenotecnum slossonae Group
T. slossonae (Banks) N, 1
Trichadenotecnum spiniserrulum Group
T. pardus Badonnel N, 2
Tribe Metylophorini
Metylophorus barretti (Banks) N, 4, 6
M. novaescotiae (Walker) N, 1, 6
M. purus (Walsh) N, 1
Tribe Cerastispsocini
Cerastipsocus trifasciatus (Provancher) N, 1, 4, 6
C. venosus (Burmeister) N, 1, 2
Subfamily Amphigerontiinae
Amphigerontia bifasciata (Latreille) N, 3
A. contaminata (Stephens) I, 5
A. infernicola (Chapman) N, 4
A. longicauda Mockford & Anonby N, 4
A. montivaga (Chapman) N, 1, 4
A. petiolata (Banks) N, 4
Blaste cockerelli (Banks) N, 4
B. garciorum Mockford N, 2, 6
B. longipennis (Banks) N, 4
B. opposita (Banks) N, 1
B. oregona (Banks) N, 5
B. osceola Mockford N, 2
B. persimilis (Banks) N, 2
B. posticata (Banks) N, 2, 6
B. quieta (Hagen) N, 1
B. subapterous (Chapman) N, 4
B. subquieta (Chapman) N, 1
Blastopsocus goodrichi Mockford N, 4
B. johnstoni Mockford N, 4
B. lithinus (Chapman) N, 1
B. semistriatus (Walsh) N, 1
B. variabilis (Aaron) N, 1
B. walshi Mockford N, 1
B. sp. N, 4

The list is based on the classification used by Lienhard and Smithers (2002), modified by the work of Yoshizawa et al. (2006) and Johnson and Mockford (2003). See text (section 6) for explanation of letter/number combinations following species names.

Table 1. Synoptic List of North American Psocoptera

A very different picture is seen in comparing the North American psocid fauna with the relatively well-studied psocid fauna of China (Li, 2002, see also Lienhard, 2003). The Chinese fauna is reported to contain 1505 species in 170 genera. The North American fauna is miniscule by comparison. A minor part of this difference may be due to over splitting at the generic and specific levels in the study of the Chinese material. Most of this huge difference must be due to historico-geographic and historico-climatic differences beyond the scope of this chapter.

Another comparison of interest is that of the Mexican fauna (faunal list in Mockford & García Aldrete, 1996) and the North America fauna. Although many species of the Mexican psocid fauna have not yet been named, what must amount to the great majority have now been recognized. The Mexican list includes 642 recent species in 97 genera and 32 families. Four families of the Superfamily Electrentomoidea (Families Musapsocidae, Troctopsocidae, Manicapsocidae, and Compsocidae) and Family Dolabellopsocidae of the Infraorder Epipsocetae reach southern Mexico from the deeper tropics but fail to reach North America. These five families account for most of the generic difference, while a significant amount the species-level difference is accounted for by the huge genus *Lachesilla*, which, though well represented in North America (75 species), has more than twice as many species in Mexico (157 species).

2. Biological aspects of the Psocoptera affecting dispersal and distribution

Psocoptera, commonly called psocids or the bark lice, are small insects, adults from the area under consideration ranging in body length from 1 to 5 mm. They are neopterous, exopterygote, acercareous (definitions in Nichols & Schuh, 1989). Adults typically have two pairs of membranous wings, but many evolutionary lines have undergone selection for wing reduction and loss. The winged forms appear to be weak flyers (Mockford, 1962) but may be carried by wind (discussed below). Nearly all are oviparous, and although ovovivipary is known, it is restricted to only two species living in North America, both of the genus *Archipsocopsis*. Many aspects of psocid biology were treated by New (1987). Immatures (nymphs) are generally cryptic in color and sometimes in form against their substrate. They feed on epiphytic and epigaeic algae and lichens, as well, in some forms, insect eggs and remains of dead insects. Mouthparts are of the chewing type (cf. Triplehorn & Johnson, 2005) with laciniae developed as rods. The latter are thought to stabilize the heavy mandibles as they bite and chew through tough material. Some 50 species have adapted to living primarily or in part in human habitations, and some of these feed primarily on farinaceous products (cf. Mockford, 1991). Psocids of all postembryonic stages have a unique apparatus in the mouthparts allowing extraction of water from the atmosphere. This involves a complex hypopharynx with a pair of lingual sclerites that are extruded with their lower surfaces out of the mouth during periods of higher relative humidity following dry periods. Water molecules accumulate on these surfaces and pass to the foregut by capillarity and action of a cibarial pump (see discussion in Lienhard, 1998: 33 - 36). This mechanism has probably allowed some forms to survive in desert regions and others to live in heated human dwellings during winter.

3. Seasonality and its adaptations

Psocids living in the northern portion of North America (Canada and the northern two to three tiers of US states) pass the winter in the egg stage. Eertmoed (1978) and Glinianaya (1975) found a temperature–dependent response of females to late-summer shortening of day length as induction of winter diapausing eggs. In northern Mexico and the extreme southern United States, numerous species of psocids are active throughout the year. In southern Arizona and southern California, several species have only a single generation per year, in winter, with eggs hatching in mid November to early December and adults appearing in late December and persisting through May (Mockford, 1984b and pers. obs.) Observations by D. Young in south-central Texas suggest a similar pattern for several species in that region (personal communication). Such a pattern permits the species to pass the hot, dry summers of these areas in the relatively persistent egg stage. Although no data are available, it is likely that an environmentally induced summer egg diapause is involved. D .J. Schmidt (unpublished MS thesis, Illinois State University, 1989) determined seasonal occurrence of 27 species of Psocoptera at the Archbold Biological Station, Lake Placid, Florida (south-central Florida). Fifteen species were winter-uniseasonal (peak of abundance between December and May). Seven species were summer-uniseasonal (peak of abundance between June and November). Three species appeared to be biseasonal, with a peak in December and a peak in June. A single species appeared to be non-seasonal, and seasonality of one could not be determined. Nearly all of the larger forms (Family Psocidae) were winter-uniseasonal.

4. Modes of dispersal

Unfortunately, this is an area about which little is known. Earlier literature on this subject was reviewed by New (1987). A regular period of flight activity is part of the life cycle of some species of psocids, but such flights usually involve only short distances. Some species are known to become part of the aerial plankton and are carried long distances in that way. A notable case is that of the (primarily) North American species *Lachesilla pacifica* Chapman. Thornton (1964) reported that a female of this species was taken on a ship's aerial trapping device, 835 km at sea from San Francisco and thought to be a genuine air capture. The species occurs regularly along the Pacific coast from Vancouver, B.C., to southern California (Mockford, 1993). Throughout that area it is represented by sexual and thelytokous (all female) populations. Temporary populations, always of the thelytokous form, become established in central Illinois and Kentucky, far to the east of the usual range (García Aldrete, 1973; Mockford, 1993). The species was also reported from the region of Geneva, Switzerland (Lienhard, 1989), where three females were taken in two successive years. In all of these cases, long-distance wind transport is the likely means of dispersal.

Other non-human modes of psocid transport, including phoresy on birds and mammals, reviewed by New (1987) are of interest, but have not been investigated in North America.

Mockford (1991) listed and keyed 50 species of psocids known to live commonly in human habitations. Many of these are cosmopolitan in distribution and are known to be spread through human commerce. The region of origin of most of those species (those designated "C" in Table I) are not known and can only be suggested in some cases where species show close relationship to forms native or endemic to particular regions.

5. Native versus introduced taxa

Mockford (1993) proposed the following criteria to determine if a species has been introduced: (1) species commonly associated with human commerce are regarded as introduced unless they have an extensive out-door distribution in the study area; (2) species for which introduction into the study area has been documented and which are not, or scarcely, otherwise present are regarded as introduced; 3) species widely distributed elsewhere, and with a very limited, coastal distribution in the study area are regarded as introduced unless the distribution in the study area appears to be part of a natural distribution largely outside the study area. The species designated I and (dom) on Table I are regarded as introduced.

6. Distribution patterns in North American Psocoptera

Table 1, the synoptic list of taxa, includes for each species its status: native (N), intercepted at a port of entry (I, followed by no number), introduced or cosmopolitan and established in a particular area (C or I, followed by a number), introduced or cosmopolitan but found only in human habitations [C or I, followed by (dom)]. The numbers refer to primary distribution patterns. Mockford (1993) recognized five of these for the North American psocid fauna. A sixth must be added for the extended definition of North America followed here. Following are the definitions of the patterns (see also map, Fig. 1).

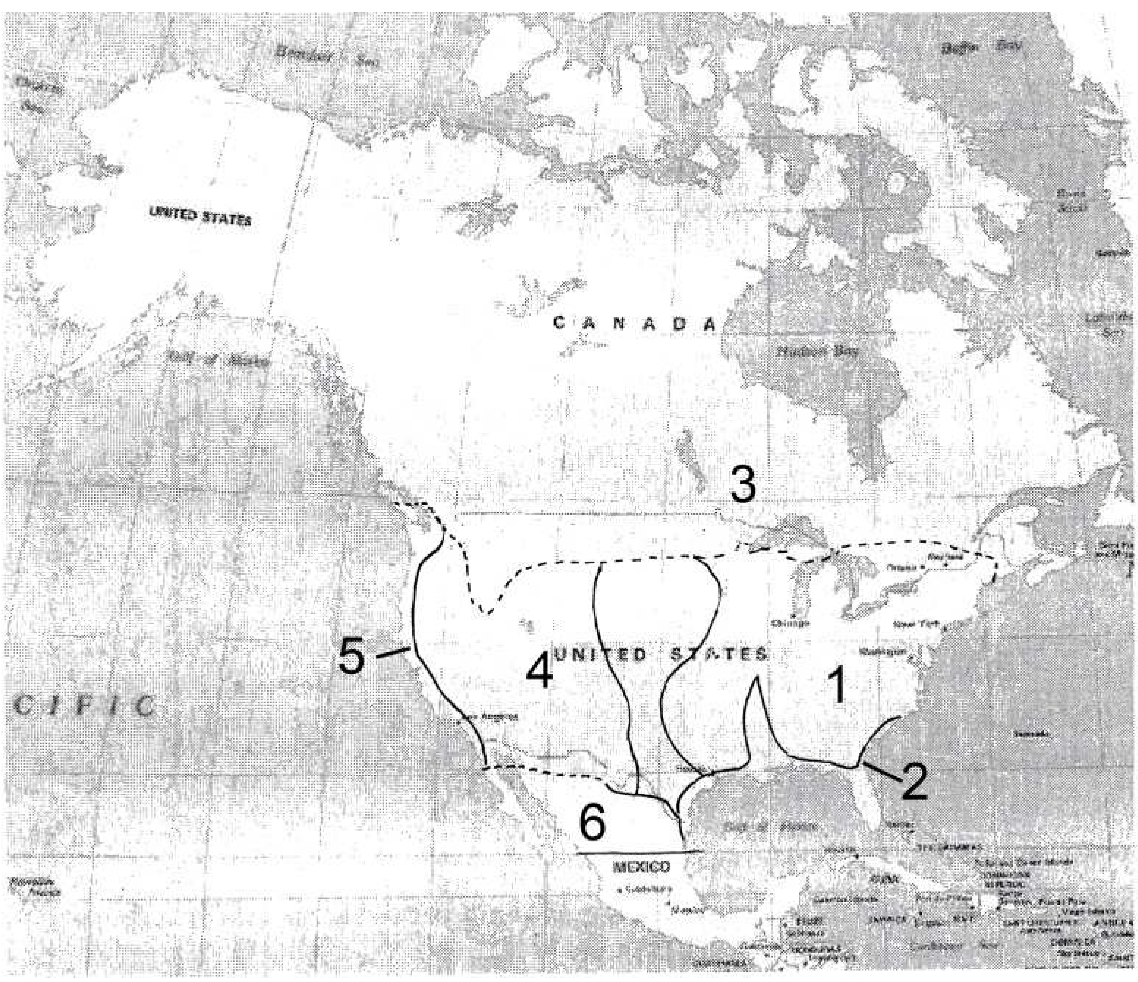

Fig. 1. Outline map of North America showing distribution patterns of Psocoptera. See text section 6 for explanation of numbers. Note an area in central United States where records are too sparse to permit assignment to a pattern.

1. The Eastern Deciduous Forest Pattern. The area corresponds closely to the Eastern Deciduous Forest as delimited by Braun (1950). Based on psocid distributions, its northern limit remains poorly understood for lack of collecting, but it clearly extends north to central Ontario and northern Minnesota. Its southern limit in the east lies in north-peninsular Florida. From there, it extends westward just off the coastal plain to the forested area of northeastern Texas. This pattern is represented by 79 species (Table 1, species designated N, 1 and I, 1) or 20.7% of the total North American fauna.
2. The Southeastern Subtropical Pattern. This pattern is coextensive with the coastal plain of the Gulf states and that of the southern Atlantic states, including essentially all of Florida extending up the Mississippi Embayment, for some species as far as southern Illinois, and up the Atlantic coast, for a few species even to Long Island. This pattern includes 88 species (Table 1, species designated N, 2, I, 2, and C, 2) or 22.7% of the North American fauna. A few of these species may, in fact, be introductions, but the criteria for recognition of introduction, discussed above, are not met. Speciation among the taxa in this pattern is discussed in Section 7.
3. The Boreal and Holarctic Pattern. This pattern is represented in North America by a very small array of species (Table 1, species designated N, 3 and I, 3), only 18, or 4.7% of the North American fauna. These are all either Holarctic in distribution or have close affinity with Holarctic species. Included here are all three of the North American species of *Mesopsocus* and five of the seven North American *Elipsocus* species.
4. The Southwestern and Rocky Mountain Pattern. This pattern is based on taxa found in the southern and central Rocky Mountains, the surrounding arid lands, and the California Sierra Nevada. Sixty-nine species (Table 1, species designated N, 4, and C, 4) are included in this pattern, or 19.8% of the North American fauna.
5. The Pacific Coast Pattern. A substantial number of species, probably including both native and introduced forms, have adapted to the mesic, in some areas highly humid, habitats of the Pacific coastal plain. Some of those taxa range eastward into the Cascade Mountains and a few even into the Rocky Mountains. Some of them are taxa also represented in Pattern 1 (see also section 7). Thirty-five species are included in this pattern (Table 1, species designated N, 5; C ,5, and I, 5) or 9.0% of the North American fauna.
6. The North-Mexican Montane areas and surrounding High Plains. Unfortunately, the western part of this interesting pattern remains rather poorly explored, and some material in collections remains to be investigated. Sixty-four species are included in this pattern (Table 1, species designated N, 6) or 16.5% of the North American fauna.

   The percentages of the total fauna noted above only reach 91.1%. The rest of the faunal list consists of intercepts at ports of entry (I , and I(dom), followed by no number on Table 1), of which there are 34 species, and cosmopolitan domestic (i.e. in human habitations) species, of which there are six (C (dom) and IC (dom) on Table 1). *Psyllipsocus ramburii* forms something of an exception to all others, being a cosmopolitan species occurring commonly in human dwellings, but also occurring in caves throughout North America.

7. Speciation in North American Psocoptera

7.1 Speciation in sexual species

The overall impression of speciation in North American Psocoptera is that there has not been a large amount of in situ differentiation. Passing through Table 1 in systematic order, the first group suggesting speciation is the *Echmepteryx hageni* complex, with three species, *E. hageni, E. intermedia,* and *E. youngi*. Undoubtedly, they are closely related, but they are all part of a much larger Antillean complex, and, indeed, *E. intermedia* also occurs in Jamaica. It seems quite possible that each of the three species may have been derived separately from Antillean ancestors.

In the genus *Rhyopsocus*, the three species *R. maculosus, R. micropterus*, and *R. texanus* appear to be closely related. The speciation events that led to their separation probably occurred in northern Mexico and adjacent southern United States. These species inhabit ground litter and pack rat nests, where humidity probably remains higher than in the surrounding xeric lands. *Rhyopsocus bentonae*, a species of peninsular Florida, southern Georgia, and the Gulf coast to Texas is part of a complex, with a second species on the Florida keys and a third in southern Mexico. The two Florida species may represent range expansions at different times of more southern species with subsequent adaptive changes.

In the genus *Psyllipsocus*, there appear to be two examples of speciation within North America, but both are currently under investigation.

In the genus *Speleketor*, the speciation events leading to the establishment of the three known species may have occurred in southwestern United States, but nymphs of a presumed fourth species of *Speleketor* have been found in a cave in Nuevo León State in northern Mexico (pers. obs.).

In the Subfamily Embidopsocinae of the Family Liposcelididae, two species, *Belaphotroctes hermosus* and *B. simberloffi*, the former of woodland ground litter in southern Texas and northern Mexico, and the latter in red mangroves on the Florida Keys, appear to be closely related (Mockford, 1972). Their speciation may have resulted from breakup of a continuous range around the Gulf of Mexico. Mockford (1993) noted the close proximity of the *Embidopsocus* species of subgroup IB (see Mockford, 1993: 78). Speciation in this subgroup has resulted in two Brazilian species, a Cuban species, and three species in North America. Of the latter three, *E. bousemani* is restricted to hilltops in the extreme southwestern Appalachian Mountains and in the Ozark hills. *Embidopsocus laticeps* is a Florida and south coastal-plain species extending north into southern Georgia and west into Louisiana. The third species, *E. mexicanus*, occurs widely in southern Mexico and is known from two localities in southeastern Texas. Oddly, a single specimen was collected at Funks Grove in central Illinois. The species of *Embidopsocus* are subcorticolous, and one species in southeastern Asia was recorded as phoretic on a migratory bird (Mockford, 1967).

In the genus *Liposcelis*, *L. pallida* and *L. villosa* appear to be closely related and may have speciated in the mountains of southwestern United States.

In the Family Archipsocidae, *Archipsocus floridanus* and *A. nomas* are probably closely related, but both are known from areas to the south of the study area, and it is likely that their speciation did not occur within the study area.

In the Family Caeciliusidae, the large genus *Valenzuela* shows a few examples of speciation in North America. *Valenzuela nadleri* and *V. totonacus* are closely related. Both are ground litter inhabitants, the former in eastern United States, and the latter in southwestern United States and Mexico. They may have had a continuous range prior to the increasingly xeric conditions of the Mexican border and Southwest. *Valenzuela boreus* and *V. croesus* are closely related, the two showing north–south replacement in eastern United States. The form currently called *V. croesus* in the Mexican mountains may prove to be a separate species. *Valenzuela flavidus* seemingly budded off two species in North America, *V. hyperboreus* in the north and *V. maritimus* on the Pacific coast. In the genus *Xanthocaecilius*, *X. microphthalmus* appears to have budded off in an isolated mountain area in Nuevo León State from a much more widely distributed species, *X. anahuacensis*, which is found throughout much of Mexico and Central America (see Mockford, 1989).

In the Family Lachesillidae, two species of *Nanolachesilla* occur in southern Florida, both on dead leaves, but one, *N. hirundo*, is restricted to palms. Other species of this genus are known from Jamaica and southern Mexico. It is likely that these two species are not sister species and that their speciational events may have occurred elsewhere, at least in part. *Lachesilla texana* may offer an example of ongoing speciation. A population presumably isolated in the southern Appalachian Mountains shows male genitalic features somewhat different from those in the population extending from central Texas to northern Mexico (Mockford & García Aldrete, 2010). Within the larger species groups of *Lachesilla*, other North American speciational events will probably be revealed when relationships are better understood.

In the Family Philotarsidae, *Philotarsus californicus* and *P. kwakiutl* are, with little doubt, sister species. The former, in California, is replaced by the latter further north along the coast and in adjacent mountains.

In the Family Myopsocidae, investigation at the alpha–taxonomic level of the genus *Lichenomima* is still in an early stage. Little can be said about speciation in the North American representatives of this group except to note that some differentiation must have occurred in southeastern (and southwestern?) United States.

In the Family Psocidae, the species of the genus *Camelopsocus* probably speciated within the study area. Here, climate and, perhaps, elevation, probably played roles in the speciation events. Two species in southern California, *C. bactrianus* and *C. hiemalis*, and one species in southern Arizona, *C. tucsonensis*, are winter species, maturing from late December to February. The other two named species, *C. monticolus* and *C. similis* are summer species found at somewhat higher altitudes (see Mockford, 1965, 1984b).

7.2 Speciation involving thelytokous parthenogenesis

Mockford (1971) reviewed parthenogenesis in psocids through the literature of 1969. The overall conclusions have changed little. Parthenogenesis in psocids is always thelytoky (female–producing), and, in general, it is obligate within the strain or species in which it occurs. Betz (1983) found four morphologically distinguishable forms of *Trichadenotecnum alexanderae*. Three of these were obligatorily thelytokous forms and would not mate with males of the sexual fourth. The latter, which proved to represent the type of *T. alexanderae*, was capable of extremely limited facultative thelytoky. He named each of the thelytokous forms as a species and concluded that each was derived from a sexual ancestor. The distributions of these species overlap broadly in eastern United States. Schmidt (1992) confirmed Betz's (1983) findings concerning morphology and reproductive type, and determined the karyotype for each of the morphospecies. One of the species, *T. castum*, proved to be triploid, for which a hybrid origin was suggested.

Several other examples of speciation in North America involve production of a thelytokous species, morphologically distinct from a closely related sexual species. In the Family Philotarsidae, *Aaroniella badonneli* and *A. maculosa* form a closely related species pair in which the former is thelytokous and the latter is sexual. In this case, the range of the sexual species is more northerly than that of the thelytokous one, although the two species overlap in distribution (see also Mockford, 1979, in which *A. badonneli* is discussed under the synonym *A. eertmoedi*).

In the Family Peripsocidae, the *Peripsocus alboguttatus* species complex consists of three sexual species and one thelytokous species. The latter, *P. maculosus*, together with its close sexual congener, *P. madescens*, occurs widely throughout eastern United States and southern Canada, both species primarily inhabiting conifers. This case seems to require further investigation.

It has long been known that infection with certain bacteria, primarily of the genus *Wolbachia*, can disable sexual reproduction in various insects, so that the infected line carries on by thelytoky. Shreve et al. (2011) reviewed this area relating to Psocoptera and noted no known cases and little likelihood of such a phenomenon in this group. Investigations on *Liposcelis bostrychophila*, a common cosmopolitan stored–product pest, have shown the presence of a *Rickettsia*–type bacterium. The domestic form of this species is obligatorily thelytokous, and Perotti et al. (2006) noted that a *Rickettsia* infection in this species is obligate for egg production. Behar et al. (in press) have shown that this *Rickettsia*, identified as *R. felis*, is present in both sexual and parthenogenetic strains of *L. bostrychophila* and so does not affect the type of reproduction. A *Wolbachia* infection has been found in a thelytokous strain of *Echmepteryx hageni* (K. Johnson, pers. comm.), but it is not known to be the causative agent of the thelytoky. It is obvious that much more investigation needs to be carried out in this field.

8. Endemic taxa above the species level

The genus *Speleketor* of the Family Prionoglarididae appears to be endemic to North America, with three species, all occurring in southwestern United States: *S. irwini* and *S. pictus* in southern California, and *S. flocki* in Arizona and Nevada (see Mockford, 1984a). The latter species is a partial cave inhabitant. *Speleketor irwini* lives in the skirts of dead leaves on native stands of the palm, *Washingtonia filifera,* in canyons. *Speleketor pictus* is known from a single specimen collected by black light, so its habitat remains unknown. It is likely that additional species will be found, and a nymph probably representing an additional species was collected in a cave near Laguna de Sánchez, Nuevo León State, Mexico. The closest relatives of this genus are the sensitibilline psocids (genera *Sensitibilla* and *Afrotrogla*) from Namibia and South Africa (see Lienhard 2007, Lienhard et al. 2010). The entire Family Prionoglarididae appear to be ancient, and Yoshizawa et al. (2006) suggest that they may be Pangaean relics.

In the Family Sphaeropsocidae, two genera are endemic to North America: *Prosphaeropsocus* and *Troglosphaeropsocus* (Mockford, 2009). The former genus, with two known species, is found in ground litter on coastal hills in central California. The latter, represented by a single male, is from a cave in northern Arizona. Mockford (2009) presented a strong argument for sister–taxa relationship of the genera *Troglosphaeropsocus* and *Badonnelia.* This would suggest great age for the resulting taxon, as *Badonnelia* is known from a north-Holarctic, primarily domestic species, and four species from southern Chile (Badonnel, 1963, 1967, 1972). This presumably extinct stem taxon and its offspring genera may represent another Pangaean relic.

In the Family Psocidae, the genus *Camelopsocus* is nearly endemic to North America, although the ranges of two of the species extend into southern Mexico. As noted above, this genus consists currently of two summer–active species widely distributed in the mountains of western United States and Mexico, and three winter–active species in deserts of southern Arizona and coastal and near–coastal scrub in southern California. This suggests late

Miocene–Pliocene adaptation of a form derived from a mountain–inhabiting ancestor to lowland areas with summer climate becoming gradually unfavorable, followed by further geographic speciation in both lowland and upland taxa. *Camelopsocus* has no close relatives in North America and appears to be closest to the Palaearctic genus *Oreopsocus*, as represented by the Egyptian species, *O. buholzeri* Lienhard.

9. Human effects

Although there are no documented cases, it is possible that a low level of extinction of psocid species has been brought about by human activities, such as extensive deforestation in the East and destruction of the tall grass prairie in the Midwest. An undescribed species of *Psocus* is known from only two females collected on tamarack (*Larix laricina*) in a bog in central Wisconsin. Is this species going extinct due to human destruction of its habitat, or will further collecting effort find it in some numbers? We do not know at present. *Valenzuela graminis* is a species of tall grass prairie remnants in central Illinois. It is persistent in these prairie remnants, and it tends to find its way into restored prairies, despite the fact that females of this species are often short-winged. It is clearly not in danger of extinction.

A glance through Table I shows that numerous species have had the opportunity to expand their ranges through the agency of human commerce. This may be viewed as a form of insurance against extinction.

10. Status of knowledge and needed research

Distributions of most North American psocid species remain poorly known. The known distributions still tend to reflect where specialists have lived rather than the true distributions of species. Much more collecting needs to be done, especially in the northern tier of US states and southern Canada, along the Atlantic and Pacific coasts, the northern and western coasts of the Gulf of Mexico, and throughout the Southwest.

Much more needs to be done to establish phylogenetic relationships, both through morphological and molecular studies. In this respect, life history studies have lagged far behind, not being a "popular" form of research.

Although funding is difficult to find for studies on Psocoptera, it is not impossible, and careers filled with new discoveries are available.

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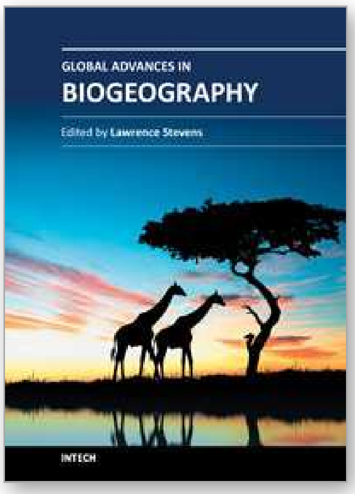

Global Advances in Biogeography

Edited by Dr. Lawrence Stevens

ISBN 978-953-51-0454-4
Hard cover, 360 pages
Publisher InTech
Published online 30, March, 2012
Published in print edition March, 2012

Global Advances in Biogeography brings together the work of more than 30 scientific authorities on biogeography from around the world. The book focuses on spatial and temporal variation of biological assemblages in relation to landscape complexity and environmental change. Global Advances embraces four themes: biogeographic theory and tests of concepts, the regional biogeography of individual taxa, the biogeography of complex landscapes, and the deep-time evolutionary biogeography of macrotaxa. In addition, the book provides a trove of new information about unusual landscapes, the natural history of a wide array of poorly known plant and animal species, and global conservation issues. This book is well illustrated with numerous maps, graphics, and photographs, and contains much new basic biogeographical information that is not available elsewhere. It will serve as an invaluable reference for professionals and members of the public interested in global biogeography, evolution, taxonomy, and conservation.

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

Edward L. Mockford (2012). Aspects of the Biogeography of North American Psocoptera (Insecta), Global Advances in Biogeography, Dr. Lawrence Stevens (Ed.), ISBN: 978-953-51-0454-4, InTech, Available from: http://www.intechopen.com/books/global-advances-in-biogeography/aspects-of-the-biogeography-of-north-american-psocoptera

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