Supporting information: 2 supplemental tables, Supplemental Material and Methods and Supplemental review of AA ecology

Table S1: Ancient asexual taxa

List of explicitly and implicitly proposed ancient asexual taxa along with their AA status according to the actual state of knowledge. Evidence for and against ancient asexuality was evaluated in each group and only well supported AAs were included in our study. The two criteria for inclusion were (1) obligately asexual reproduction, i.e. the absence of common or rare/cryptic sexual events, or derived forms of genetic exchange, for (2) at least 1 million years.

Taxon	**Ancient asexuality**	**Explicitly proposed in**	**Evidence against**	**Evidence for**
Confirmed ancient asexuals				
Rotifera: **Bdelloidea**	YES	Maynard Smith, 1986	**Domesticated horizontally transferable transposons** (Arkhipova & Meselson, 2005; Gladyshev & Arkhipova, 2007; Gladyshev, Meselson & Arkhipova, 2007); **enigmatic mentions of observed males** (Welch et al-, 2009); **evidence of allele sharing** (Signorovitch et al., 2015)	**Large and diverse clade** (Segers, 2007, 2008); **monophyletic** (Melone & Ricci, 1995; Wallace et al., 1996; Welch & Meselson, 2000); **asexual radiation** (Ricci, 1987; Birky et al., 2005; Pouchkina-Stantcheva et al., 2007); **frequency of hypothetical males would be so low they would be effectively asexual** (Birky, 2010); **very old** (Poinar & Ricci, 1992; Waggoner & Poinar, 1993; Welch & Meselson, 2000); **apomixis** (Hsu, 1956a, b); **accumulation of moderately deleterious mutations** (Barraclough et al., 2007); **Meselson effect** (Welch & Meselson, 2000; Welch et al., 2004b); **degenerated tetraploids** (Welch et al., 2004a, 2009; Welch et al., 2008; Hur et al., 2009); **specialization of collinear genes** (Pouchkina-Stantcheva et al., 2007; Welch et al., 2009); **functional haploidization** (Arkhipova & Meselson, 2000; Welch & Meselson, 2000; Gladyshev & Meselson, 2008); **unidentifiable homological pairs of chromosomes** (Welch & Meselson, 1998); **genome structure incompatible with meiosis** (Flot et al., 2013); **absence of vertically transferable transposons** (Arkhipova

				& Meselson, 2000, 2005); **allele sharing due to horizontal gene transfer** (Debortoli et al., 2016)
Arthropoda: Ostracoda: **Darwinulidae**	YES	Judson & Normark, 1996	**Vertically transferable transposons** (Schön & Arkhipova, 2006); **rare males** (Rossetti & Martens, 1996; Smith et al., 2006; Schön et al., 2009); **uncertain Meselson effect** (Schön et al., 1998); **slow speed of molecular evolution** (Gandolfi et al., 2001; Schön & Martens, 2003); **high homozygosity** (Martens, 1998); **low morphological and genetic diversity** (Rossetti & Martens, 1996, 1998; Schön et al., 1998)	**Large and diverse clade** (Martens et al., 2008; Martens & Savatenalinton, 2011); **monophyletic** (Schön et al., 2003, 2009; Yamaguchi & Endo, 2003; Wysocka et al., 2006; Yu et al., 2006; Yamada, 2007; Tinn & Oakley, 2008); **rare males spanandric** (Rossetti & Martens, 1996; Smith et al., 2006; Schön et al., 2009); **frequency of hypothetical males would be so low they would be effectively asexual** (Birky, 2010); **probably apomixis** (Butlin et al., 1998); **absence of automixis** (Schön et al., 1998); **absence of polyploidy** (Rossi et al., 1998); **absence of fossil males since the end of Permian /Triassic?/** (Molostovskaya, 2000; Martens et al., 2003); **millions of years old fossils classifiable into recent species and genera** (Straub, 1952; Abushik, 1990; Martens et al., 1997; Martens et al., 1998a; Martens et al., 2003; Smith et al., 2006); **very old according to the molecular clock** (Martens et al., 2005); **domesticated transposons** (Schön & Arkhipova, 2006); **genetic homogeneity proven not to be the consequence of automixis or recombination** (Schön & Martens, 2003); **unidentifiable homological pairs of chromosomes** (Tétart, 1978); **absence of hybridization among lineages** (Rossi et al., 1998)
Arthropoda: Acari: Oribatidae: **Nanhermanniidae, Malaconothridae, Trhypochthoniidae, Camisiidae and majority of Nothridae; Brachychthoniidae and Lohmanniidae**	YES	Judson & Normark, 1996	**Meselson effect not observed** (Schaefer et al., 2006); **rare males** (Palmer & Norton, 1990, 1991; Norton et al., 1993); **possibly revolution of sexuality** (Domes et al., 2007b)	**Large and diverse clades** (Norton et al., 1993; Subías, 2004; Norton & Behan-Pelletier, 2009); **asexual radiations** (Palmer & Norton, 1991); **rare males spanandric** (Taberly, 1988; Palmer & Norton, 1990, 1991, 1992; Norton et al., 1993); **Meselson effect not observed because of automixis with terminal fusion of gametes** (Taberly, 1987; Wrensch, Kethley & Norton, 1994; Schaefer et al., 2006) **and mostly inverted meiosis** (Wrensch et al., 1994; Heethoff, 2004; Laumann et al., 2008); **very old** (Krivolutsky & Druk, 1986; Maraun et al., 2003, 2004; Heethoff et al., 2007; Laumann et al., 2007) **+ not very good colonizers** (Skubala & Gulvik, 2005; Domes et al., 2007c; Cianciolo, 2009) **and biogeographic distribution corresponds to continental drift** (Hammer & Wallwork, 1979; Heethoff, 2004; Heethoff

				et al., 2007); **absence of sexual clades closely related to asexual lineages** (Norton et al., 1993; Maraun et al., 2004); **absence of recombination** (Palmer & Norton, 1992; Heethoff, 2004; Schaefer et al., 2006); **reevolution of sexuality is exceptional and uncertain** (Domes et al., 2007b)
Arthropoda: Acari: Endeostigmata: **Nematalycidae, Proteonematalycidae; Oehserchestidae, Granjeanicidae; *Alicorhagia*, *Stigmalychus***	YES	Judson & Normark, 1996	**Poorly understood** (Walter, 2009); **rare males** (Norton et al., 1993)	**Rare males are spanandric**; **analogies with asexual Oribatidae (frequency of males, their spanandric character, ecology, distribution, population genetics etc.)** (Norton et al., 1993)
Arthropoda: Acari: Trombidiformes: **Lordalycidae; Pomerantziidae**	YES	Judson & Normark, 1996	**Poorly understood** (Walter et al., 2009); **rare males** (Norton et al., 1993)	**Rare males are spanandric**; **analogies with asexual Oribatidae (frequency of males, their spanandric character, ecology, distribution, population genetics etc.)** (Norton et al., 1993)
Arthropoda: Phasmatodea: ***Timema*: *Timema tahoe*, *Timema monikensis*, *Timema genevieve***	YES	Sandoval, Carmean & Crespi, 1998	**Rare males** (Vickery & Sandoval, 2001; Law & Crespi, 2002a); **no signs of haploidization** (Schwander & Crespi, 2009a)	**Obligatory parthenogenesis** (Sandoval & Vickery, 1996; Sandoval et al., 1998; Law & Crespi, 2002a, b; Schwander & Crespi, 2009a); **apomixis** (Crespi & Sandoval, 2000; Law & Crespi, 2002a; Schwander & Crespi, 2009a; Schwander, Henry & Crespi, 2011); **asexual females do not mate with sexual males** (Sandoval et al., 1998); **rare males spanandric** (Law & Crespi, 2002a; Schwander & Crespi, 2009a); **degeneration of sexual traits in females** (Schwander et al., 2013); **recombination, haploid gametes and meiosis never observed** (Schwander et al., 2010, 2011); **degradation of chromosome pairing in *Timema genevieve*** (Schwander & Crespi, 2009a); **very old** (Law & Crespi, 2002a, b; Schwander et al., 2011); **extinct or undiscovered mother species improbable** (Sandoval et al., 1998); **Meselson effect** (Schwander et al., 2011); **slower mutation speed and more deleterious mutations in asexual lineages** (Schwander et al., 2011; Henry, Schwander & Crespi, 2012)
Mollusca: Bivalvia: ***Lasaea* except *Lasaea australis* and *Lasaea colmani***	YES	Ó Foighil & Smith, 1995	**Polyphyletic asexual lineages probably originated in hybridizations** (Thiriot-Quivreux, 1992; Ó Foighil & Smith, 1995; Taylor & Ó Foighil, 2000; Li et al., 2013); **sperm still able to bind to an egg and penetrate it** (Ó Foighil,	**Pseudogamous self-fertilizing hermaphrodites /autogynogenesis/** (Ó Foighil & Eernisse, 1988; Ó Foighil & Thiriot-Quiévreux, 1991, 1999; Ó Foighil & Smith, 1995; Taylor & Ó Foighil, 2000); **no outcrossing** (Ó Foighil, 1988); **male genetic material from sperm never transmit**

			1987); **the age estimated from biogeography could be an artefact if they are shown up to be good colonizers in ecological timescales** (Taylor & Ó Foighil, 2000)	**to offspring** (Ó Foighil & Thiriot-Quiévreux, 1991); **minimal male reproductive allocation, sperm are few and degenerated** (Ó Foighil, 1985; Beauchamp, 1986; McGrath & Ó Foighil, 1986); **no specialized sexual structures** (Ó Foighil & Eernisse, 1988); **almost certainly apomixis** (Ó Foighil & Thiriot-Quiévreux, 1991); **meiosis and segregation of chromosomes never observed** (Ó Foighil & Eernisse, 1988; Thiriot-Quivreux et al., 1988; Ó Foighil & Thiriot-Quiévreux, 1991); **adaptation and differentiation in asexuality** (Ó Foighil & Eernisse, 1988; Ó Foighil & Smith, 1996; Taylor & Ó Foighil, 2000; Li et al., 2013) **including ecological specializations** (Crisp & Standen, 1988; Tyler-Walters & Davenport, 1990); **polyploidy** (Ó Foighil & Smith, 1995); **variable count of chromosomes, frequent non-pairing chromosomes, impossibility of meiosis** (Thiriot-Quivreux et al., 1988; Ó Foighil & Thiriot-Quiévreux, 1991, 1999); **very old** (Ó Foighil & Smith, 1995, 1996; Ó Foighil & Jozefowicz, 1999; Li et al., 2013); **absence of cosmopolitan lineages, no rapid colonization** (Taylor & Ó Foighil, 2000); **comparable substitution speeds of sexual and asexual lineages** (Ó Foighil & Smith, 1995; Li et al., 2013); **colonization of large areas by rafting in direct-developing asexuals, long time ago when the ocean currents were different** (Ó Foighil & Jozefowicz, 1999); **repeated transitions between sexuality and asexuality, transfer of male genetic material or parallel neutral evolution highly improbable** (Ó Foighil & Smith, 1995); **undiscovered sexual lineages improbable** (Ó Foighil & Smith, 1995; Taylor & Ó Foighil, 2000)
Polypodiophyta: Vittariaceae: ***Vittaria appalachiana***	YES	Farrar, 1978	**Retrotransposons** (Docking et al., 2006); **rarely observed sporophytes** (Farrar, 1978; Caponetti et al., 1982)	**Exclusively asexual gametophyte** (Farrar, 1967); **asexual reproduction by gemmae and fission of thallus** (Farrar, 1974); **monophyletic** (Farrar, 1978, 1985, 1990); **rare sporophytes always abortive** (Farrar, 1978; Caponetti et al., 1982); **very old** (Docking et al., 2006) **+ most probably sister to some central- or south-American species** (Farrar, 1985) **+ sporophytes do not tolerate freezing, very limited migration and colonization, geographical distribution is relict of that of its mother species** (Farrar, 1978; Parks & Farrar, 1984; Farrar, 1990, 1998); **internally genetically uniform but disparate populations** (Farrar, 1978, 1985);

				absence of gene flow (Farrar, 1990); **adaptations in asexual state** (Farrar, 1985, 1990); **transposons probably domesticated** (Schön & Arkhipova, 2006)
Refused and contested ancient asexuals				
Polypodiophyta: Hymenophyllaceae: ***Trichomanes intricatum***	NO	Judson & Normark, 1996	**Overestimated age** (Ebihara et al., 2008)	**Obligately asexual** (Farrar, 1990, 1992)
Chordata: Lissamphibia: ***Ambystoma***	NO	Spolsky, Phillips & Uzzell, 1992	**Transfer of paternal genetic information from sperm in gynogenesis** (Hedges et al., 1992; Spolsky et al., 1992; Bogart et al., 2007)	**Gynogenetic clade old up to 3.5 MY** (Bi & Bogart, 2010; Bogart et al., 2007)
Chordata: Teleostei: ***Poeciliopsis*** **lineage MO/II**	NO	Judson & Normark, 1996	**Overestimated age** (Mateos & Vrijenhoek, 2002)	**Old obligately asexual lineage** (Quattro et al., 1992)
Arthropoda: Hemiptera: ***Trama***	NO	Moran, 1992	**Not obligately parthenogenetic – sexual populations** (Verma, 1969; Blackman, De Boise & Czylok, 2001)	**Obligately parthenogenetic populations** (Moran, 1992; Normark, 1999; Blackman, Spence & Normark, 2000)
Arthropoda: Hemiptera: ***Neotrama***	NO	Moran, 1992	**Not obligately parthenogenetic – sexual populations** (Verma, 1969; Normark & Moran, 2000)	**Obligately parthenogenetic populations** (Moran, 1992; Normark, 1999; Blackman et al., 2000)
Arthropoda: Hemiptera: ***Aspidiotus nerii***	NO	Provencher et al., 2005	**Uncertain age** (Provencher et al., 2005)	**Old obligately asexual lineage** (Provencher et al., 2005)
Arthropoda: Hemiptera: ***Rhopalosiphum padi***	NO	Simon et al., 1996	**Repeated generation of asexual lineages, hybridization, production of fertile males, gene flow, asexual lineages too young** (Simon et al., 1999; Delmotte et al., 2001; Delmotte et al., 2003)	**Old obligately asexual lineages** (Simon et al., 1996; Simon et al., 1999; Delmotte et al., 2001); **possibly Meselson effect** (Halkett et al., 2005)

Arthropoda: Hemiptera: **Adelgidae**	NO	Schwander & Crespi, 2009b	**Insufficient information** (Havill et al., 2007)	**Possibly old obligately asexual lineages** (Havill et al., 2007)
Arthropoda: Coleoptera: ***Aramigus***	NO	Judson & Normark, 1996	**Overestimated age** (Normark & Lanteri, 1998)	**Old obligately asexual lineage** (Normark, 1996)
Arthropoda: Coleoptera: ***Calligrapha***	NO	Gomez-Zurita et al., 2006	**Uncertain age** (Gomez-Zurita et al., 2006), **possible gene flow** (Montelongo & Gomez-Zurita, 2015)	**Old obligately asexual lineages** (Gomez-Zurita et al., 2006)
Arthropoda: Coleoptera: ***Otiorhynchus***	NO	Schwander & Crespi, 2009b	**Insufficient information** (Stenberg & Lundmark, 2004)	**Possibly old obligately asexual lineages** (Stenberg & Lundmark, 2004)
Arthropoda: Coleoptera: ***Naupactus leucoloma***	NO	Mayr, 1963	**Not obligately parthenogenetic – sexual populations** (Lanteri & Marvaldi, 1995)	**Obligately parthenogenetic populations** (Mayr, 1963)
Arthropoda: Phasmatodea: ***Bacillus atticus***	NO	Normark, Judson & Moran, 2003	**Uncertain age** (Mantovani et al., 2001)	**Old obligately asexual lineage** (Mantovani et al., 2001)
Arthropoda: Lepidoptera: **Naryciinae**	NO	Schwander & Crespi, 2009b	**Numerous recent transfers to asexuality, overestimated age** (Elzinga et al., 2013)	**Old obligately asexual lineages** (Grapputo et al., 2005)
Arthropoda: Ostracoda: ***Heterocypris incongruens***	NO	Chaplin & Hebert, 1997	**Overestimated age** (Tétart, 1978; Chaplin & Hebert, 1997; Martens et al., 1998b)	**Old obligately asexual lineage** (Chaplin & Hebert, 1997; Butlin et al., 1998)
Arthropoda: Ostracoda: ***Eucypris virens***	NO	Butlin et al., 1998	**Overestimated age** (Tétart, 1978; Martens et al., 1998b; Bode et al., 2010), **possible gene flow** (Schön et al., 2000)	**Old obligately asexual lineage** (Butlin et al., 1998; Bode et al., 2010)

Arthropoda: Anostraca: ***“Artemia parthenogenetica”***	NO	Judson & Normark, 1996	**Overestimated age** (Hebert et al., 2002), **not monophyletic** (Nascetti et al., 2003; Baxevanis et al., 2006; Muñoz et al., 2010)	**Old obligately asexual lineage** (Perez et al., 1994)
Arthropoda: Acari: ***Protogamasellus***	NO	Norton et al., 1993	**Arrhenotoky** (Afifi et al., 1986)	**Obligately parthenogenetic** (Norton et al., 1993)
Arthropoda: Acari: ***Gamasellodes***	NO	Norton et al., 1993	**Arrhenotoky** (Afifi et al., 1986)	**Obligately parthenogenetic** (Norton et al., 1993)
Arthropoda: Acari: ***Geholaspis***	NO	Norton et al., 1993	**Large proportion of males in some populations** (Gwiazdowicz & Klemt, 2004)	**Obligately parthenogenetic** (Norton et al., 1993)
Arthropoda: Acari: ***Trachytes***	NO	Norton et al., 1993	**Sexual** (Bloszyk & Szymkowiak, 1996; Bloszyk et al., 2004)	**Obligately parthenogenetic** (Norton et al., 1993)
Mollusca: Gastropoda: **Thiaridae**	NO	Morrison, 1954	**No larger lineage is obligately parthenogenetic – sexual populations** (Heller & Farstey, 1990)	**Obligately parthenogenetic populations** (Morrison, 1954)
Mollusca: Gastropoda: ***Campeloma parthenum***	NO	Normark et al., 2003	**Repeated transfers to asexuality, uncertain age of asexual lineages, possibility of hybridization** (Johnson & Bragg, 1999; Johnson, 2006)	**Old obligately asexual lineages** (Johnson & Bragg, 1999); **Meselson effect** (Johnson, 2006)
Mollusca: Gastropoda: ***Potamopyrgus antipodarum***	NO	Neiman, Jokela & Lively, 2005	**Unreliable age estimation** (Neiman et al., 2005); **obligatory asexuality questioned** (Neiman & Lively, 2005; Neiman et al., 2012)	**Old obligately asexual lineages** (Neiman & Lively, 2004; Neiman et al., 2005)
Gastrotricha: **Chaetonida**	NO	Stanley, 1979	**Facultative parthenogenesis** (Thorp & Covich, 1991; Ricci & Balsamo, 2000; Weiss, 2001)	**Obligately parthenogenetic** (Pilato, 1979; Stanley, 1979)

Tardigrada: ***Echiniscus testudo***	NO	-	**Overestimated age** (Jorgensen, et al., 2007)	**Old obligately asexual lineage** (Miller et al., 1999)
Nematoda: Heteroderidae: ***Meloidogyne***	NO	Judson & Normark, 1996	**Overestimated age** (Trudgill & Blok, 2001; Lunt, 2008)	**Old obligately asexual lineage** (Triantaphyllou, 1981; Castagnonesereno et al., 1993; Tigano et al., 2005)
Platyhelmintes: Turbellaria: ***Schmidtea polychroa***	NO	-	**Overestimated age** (Pongratz et al., 2003)	**Old obligately asexual lineage** (Pongratz et al., 2003)
Cnidaria: **Myxozoa**	NO	-	**Evidence of sexual process** (Morris, 2012)	**Sexual process never observed**
Placozoa	NO	Schurko, Neiman & Logsdon, 2009	**Evidence of sexual process** (Signorovitch et al., 2005)	**Sexual process never observed**
Glomeromycota: **Glomales**	NO	Judson & Normark, 1996	**The evidence of recombination and sexual process** (Vandenkoornhuyse et al., 2001; Gandolfi et al., 2003; Croll & Sanders, 2009; Halary et al., 2011); **meiotic genes** (Corradi & Lildhar, 2012; Tisserant et al., 2013)	**Very old obligately asexual lineage** (Remy et al., 1994; Rosendahl & Taylor, 1997; Stukenbrock & Rosendahl, 2005; Croll & Sanders, 2009); **vegetative incompatibility** (Giovannetti et al., 2003)
Basidiomycota: **Lepiotaceae**	NO	Judson & Normark, 1996	**The evidence of recombination** (Mueller, 2002; Doherty et al., 2003; Mueller et al., 2005; Mikheyev et al., 2006); **formation of sexual structures** (Mueller, 2002; Mueller et al., 2005); **absence of Meselson effect** (Mueller et al., 1998)	**Old obligately asexual lineages** (Chapela et al., 1994; Hinkle et al., 1994; Mueller et al., 1998)
Basidiomycota: **Tricholomataceae**	NO	Judson & Normark, 1996	**Evidence of recombination** (Mueller, 2002; Mueller et al., 2005; Mikheyev et al., 2006); **formation of sexual structures** (Mueller, 2002; Mueller et al., 2005); **ants are able to change among related strains of fungus** (Villesen et al., 2004)	**Old obligately asexual lineages** (Chapela et al., 1994; Hinkle et al., 1994; Mueller et al., 1998)

Ascomycota: **Ophiostomatales**	NO	Normark et al., 2003	**Uncertain age – horizontal transfer among bark beetles** (Farrell et al., 2001)	**Old obligately asexual lineages** (Farrell et al., 2001)
Ascomycota: ***Aspergillus fumigatus***	NO	-	**Evidence of sexual process** (O'Gorman et al., 2009)	**Sexual process never observed**
Ascomycota: ***Candida albicans***	NO	Schurko et al., 2009	**Evidence of recombination, probably facultative sexual** (Graser et al., 1996; Tibayrenc, 1997; Hull & Johnson, 1999; Tzung et al., 2001; Odds et al., 2007); **transposons** (Goodwin & Poulter, 2000)	**Parasexual cycle** (Bennett & Johnson, 2003; Forche et al., 2008); **clonal** (Graser et al., 1996; Tibayrenc, 1997)
Zygomycota: **Microsporidia (*Encephalitozoon cuniculi*)**	NO	Schwander & Crespi, 2009b	**Repeated recent loss of sexuality, overestimated age** (Ironside, 2007; Haag et al., 2013); **meiotic genes** (Biderre et al., 1999; Ramesh et al., 2005; Cuomo et al., 2012)	**Old obligately asexual lineages** (Tay et al., 2005)
Excavata: Trichomonadida: ***Trichomonas vaginalis***	NO	Schurko et al., 2009	**Meiotic genes, transposons** (Carlton et al., 2007; Malik et al., 2008); **evidence for recombination and sexual process** (Drmota & Kral, 1997; Hampl et al., 2001)	**Clonal** (Tibayrenc et al., 1990; Tibayrenc et al., 1991)
Excavata: **Diplomonadida (*Giardia intestinalis*)**	NO	Normark et al., 2003	**Evidence of sexual process** (Bernander et al., 2001; Morrison et al., 2007); **meiotic genes** (Ramesh et al., 2005; Malik et al., 2008); **population genetics signs of sex** (Cooper et al., 2007; Andersson, 2012)	**Obligately parthenogenetic** (Dacks & Roger, 1999); **domesticated transposons** (Arkhipova & Morrison, 2001)
Excavata: **Kinetoplastea (*Trypanosoma cruzi*, *Trypanosoma brucei*)**	NO	Schurko et al., 2009	**Meiotic genes, transposons** (Berriman et al., 2005; El-Sayed et al., 2005; Weedall & Hall, 2015); **evidence for recombination and sexual process** (MacLeod et al., 2005); **meiotic cycle and haploid gametes** (Peacock et al., 2011, 2014)	**Clonal** (Tibayrenc et al., 1990, 1991); **parasexual process** (Gaunt et al., 2003), **few or no recombination** (Oliveira et al., 1998)
Excavata: **Heterolobosea (*Naegleria gruberi*)**	NO	-	**Meiotic genes** (Fritz-Laylin et al., 2010)	**Sexual process never observed**

Excavata: **Jakobida**	NO	-	**Genes for plasmogamy and karyogamy** (Speijer et al., 2015)	**Sexual process never observed**
Excavata: **Malawimonadida**	NO	-	**Genes for plasmogamy and karyogamy** (Speijer et al., 2015)	**Sexual process never observed**
Alveolata: Dinoflagellata: ***Symbiodinium***	NO	-	**Meiotic genes** (Chi et al., 2014)	**Sexual process never observed**
Alveolata: **Apicomplexa (*Toxoplasma gondii*)**	NO	Schurko et al., 2009	**Evidence for recombination and sexual process** (Tibayrenc et al., 1990; Howe & Sibley, 1995; Grigg et al., 2001; Heitman, 2006; Khan et al., 2007); **meiotic genes** (Weedall & Hall, 2015)	**Clonal** (Tibayrenc et al., 1990, 1991; Howe & Sibley, 1995); **old** (Sibley & Boothroyd, 1992; Khan et al., 2007)
Stramenopila: **Eustigmatophyceae (*Nannochloropsis oceanica*)**	NO	-	**Related species sexual** (Radakovits et al., 2012)	**Haploid, sex process never observed, few mitotic genes** (Pan et al., 2011)
Stramenopila: **Parmales - Bolidophyceae**	NO	-	**Haploid and diploid stages of one group** (Kessenich et al., 2014)	**Sexual process never observed**
Rhizaria: **Foraminifera (*Reticulomyxa filosa*)**	NO	-	**Meiotic genes** (Glöckner et al., 2014)	**Sexual process never observed**
Chromista: **Cryptophyta (*Chroomonas acuta*; *Proteomonas sulcata*)**	NO	-	**Haploid gametes, syngamy** (Kugrens & Lee, 1988); **haploid and diploid stages** (Hill & Wetherbee, 1986)	**Sexual process never observed**
Chlorophyta: **Glaucophyta (*Cyanophora paradoxa*)**	NO	-	**Genes for plasmogamy and karyogamy** (Speijer et al., 2015)	**Sexual process never observed**

Chlorophyta: Prasinophyceae: ***Ostreococcus tauri***	NO	-	**Evidence of sexual process** (Grimsley et al., 2010)	**Sexual process never observed**
Chlorophyta: **Trebouxiophyceae (*Chlorella variabilis*)**	NO	-	**Evidence of sexual process** (Blanc et al., 2010); **meiotic genes** (Fucikova et al., 2015)	**Sexual process never observed**
Amoebozoa: **Entamoebida (*Entamoeba histolytica*)**	NO	Normark et al., 2003	**Evidence of sexual process** (Blanc et al., 1989); **meiotic genes** (Ramesh et al., 2005)	**Obligately parthenogenetic** (Dacks & Roger, 1999)
Opisthokonta: Ichthyosporea: ***Pseudoperkinsus tapestis***	NO	-	**Evidence of sexual process** (Marshall & Berbee, 2010)	**Sexual process never observed**
Opisthokonta: **Choanoflagelata (*Monosiga brevicolis*; *Salpingoeca rosetta*)**	NO	-	**Meiotic genes** (Carr et al., 2010); **retrotransposons** (Carr et al., 2008); **evidence of sexual process** (Levin & King, 2013)	**Sexual process never observed**
Opisthokonta: **Filasterea (*Capsaspora owczarzaki*)**	NO	-	**Meiotic genes** (Suga et al., 2013)	**Sexual process never observed**
Newly proposed ancient asexuals				
Ophistokonta: **Cristidiscoidea (*Fonticula alba*)**	?	Speijer et al., 2015	**Poorly understood**	**Sexual process never observed; genes for plasmogamy and karyogamy absent** (Speijer et al., 2015)
Ophistokonta: **Ichthyosporea (*Sphaeroforma arctica*)**	?	Speijer et al., 2015	**Poorly understood**	**Sexual process never observed; genes for plasmogamy and karyogamy absent** (Speijer et al., 2015)

Apusomonadida (*Thecamonas trahens*)	?	Speijer et al., 2015	**Poorly understood**	**Sexual process never observed; genes for plasmogamy and karyogamy absent** (Speijer et al., 2015)
Alveolata: Ciliata: **amicronucleate ciliates**	?	Speijer et al., 2015	**Poorly understood**	**Clonal, unable to undergo meiosis, lineages very old /?/** (Doerder, 2014); **“auto-recombination” of macronuclei** (Nowacki et al., 2008, 2011)
Breviatea, Ancyromonadida, Mantamonadida, Rigifilida, Collodictyonida, Telonemia, Centrohelida, Palpitomonadea, Katablepharida, Picozoa	??	Speijer et al., 2015	**Extremely poorly understood**	**Sexual process never observed**

Table S2: Sexual controls

List of sister or closely related, ecologically comparable, sexual taxa of the ancient asexuals included in our study. In those individual cases in which the phylogenetic relations between the sexual and asexual lineages were not entirely clear, we used the closest possible comparable clades, i.e. clades proven to be closely related and broadly comparable in terms of their ecology—aquatic for aquatic AAs, benthic for benthic AAs, terrestrial for terrestrial AAs, parasitic for parasitic AAs etc. In polyphyletic AA groups, monophyletic AA lineages and their sexual controls are identified.

Ancient asexual taxon	*Sexual control*	*Reasoning*
Bdelloidea	**Monogononta**	**Bdelloidea are monophyletic within Rotifera** (Melone & Ricci, 1995; Wallace et al., 1996; Welch & Meselson, 2000). **Phylogenetic relationships of the clades within Rotifera are unclear. Monogononta are ecologically comparable and closely related to Bdelloidea** (Garey et al., 1996; Welch, 2000; Herlyn et al., 2003; Garcia-Varela & Nadler, 2006; Sorensen & Giribet, 2006; Witek et al., 2008; Min & Park, 2009; Fontaneto & Jondelius, 2011; Lasek-Nesselquist, 2012).
Darwinuloidea	**Cypridoidea**	**Darwinuloidea consist of a single recent family Darwinulidae and are monophyletic within Ostracoda** (Schön et al., 2003, 2009; Yamaguchi & Endo, 2003; Wysocka et al., 2006; Yu et al., 2006; Yamada, 2007; Tinn & Oakley, 2008). **Phylogenetic relationships of the clades within Ostracoda are unclear. Cypridoidea are ecologically comparable and closely related to Darwinuloidea** (Scott, 1961; Maddocks, 1976; Martens et al., 1998a, b; Schön et al., 2003, 2009; Yamaguchi & Endo, 2003; Liebau, 2005; Wysocka et al., 2006; Yu et al., 2006; Tinn & Oakley, 2008).
Oribatidae - Nanhermanniidae, Malaconothridae, Trhypochthoniidae, Camisiidae, larger part of Nothridae	**Brachypylina**	**Nanhermanniidae, Malaconothridae, Trhypochthoniidae, Camisiidae and Nothridae are included into taxon Desmonomata, which is of unclear monophyly within Oribatidae. Phylogenetic relationships of the clades within Oribatidae are quite unclear. All clades within Oribatidae are ecologically comparable. Besides several isolated sexual species, Desmonomata are probably related to sexual crown group Brachypylina** (Norton et al., 1993; Norton, 1994; Judson & Normark, 1996; Normark et al., 2003; Domes et al., 2007a, b; Heethoff et al., 2009; Norton & Behan-Pelletier, 2009; Dabert et al., 2010).
Oribatidae - Brachychthoniidae	**Mesoplophoridae**	**Brachychthoniidae are probably monophyletic within Enarthronota. Phylogenetic relationships within Oribatidae are quite unclear. All clades within Oribatidae are ecologically comparable. Mesoplophoridae are closely related to Brachychthoniidae** (Norton et al., 1993; Norton, 1994; Judson & Normark, 1996; Normark et al., 2003; Domes et al., 2007a, b; Heethoff et al., 2009; Norton & Behan-Pelletier, 2009; Dabert et al., 2010).
Oribatidae - Lohmanniidae	**Remaining lineages of Enarthronota**	**Lohmanniidae are probably monophyletic within Enarthronota. Phylogenetic relationships within Oribatidae are quite unclear. All clades within Oribatidae are ecologically comparable. Lohmanniidae are basal lineage of Enarthronota and thus they can be compared only with its remaining lineages**

		(Norton et al., 1993; Norton, 1994; Judson & Normark, 1996; Normark et al., 2003; Domes et al., 2007a, b; Heethoff et al., 2009; Norton & Behan-Pelletier, 2009; Dabert et al., 2010).
Endeostigmata - Nematalycidae and Proteonematalycidae	**Micropsammidae**	**The sister group of Nematalycidae and Proteonematalycidae is Micropsammidae, which is also ecologically comparable** (Norton et al., 1993; Walter et al., 2009).
Endeostigmata - Grandjeanicidae and Oehserchestidae	**Terpnacaridae**	**The sister group of Grandjeanicidae and Oehserchestidae is Terpnacaridae, which is also ecologically comparable** (Norton et al., 1993; Walter et al., 2009).
Endeostigmata – genera *Alicorhagia* and *Stigmalychus* (crown group of Alicorhagiidae)	***Epistomalycus*/ Oribatidae + Astigmata**	**Genera Alicorhagia and Stigmalychus constitute the crown group of Alicorhagiidae. It is possible to compare them with the basal sexual genus of Alicorhagiidae (Epistomalycus). Alternatively, they can be compared with closely related groups Oribatidae + Astigmata** (Norton et al., 1993; Walter et al., 2009). **All mentioned clades are ecologically comparable. Both options were evaluated in the study.**
Trombidiformes - Lordalycidae	**Sphaerolichidae + Prostigmata**	**Lordalycidae are closely related to Sphaerolichidae and Prostigmata, which are also ecologically comparable** (Norton et al., 1993; Walter et al., 2009).
Trombidiformes - Pomerantziidae	**Pterygosomatoidea, Raphignathoidea, Cheyletoidea and Tetranychoidea/ Stigmocheylidae, Pseudocheylidae, Heterostigmata and Paratydelidae**	**Pomerantziidae are either basal in the clade including Pterygosomatoidea, Raphignathoidea, Cheyletoidea and Tetranychoidea or the clade including Stigmocheylidae, Pseudocheylidae, Heterostigmata and Paratydelidae** (Norton et al., 1993; Walter et al., 2009). **All mentioned clades are ecologically comparable. Both options were evaluated in the study.**
Vittaria appalachiana	***Vittaria linneata*/ *Vittaria graminifolia***	***Vittaria appalachiana* is a monophyletic clade** (Farrar, 1978, 1985, 1990). **Possible mother or sister lineages are *Vittaria linneata*** (Gastony, 1977), ***Vittaria graminifolia*** (Crane, 1997) **or (most probably) some yet unidentified neotropical species** (Farrar, 1985, 1990); **moreover, the origin of *Vittaria appalachiana* in interspecific hybridization cannot be ruled out** (Ebihara et al., 2009). **All mentioned clades are ecologically comparable. All options were evaluated in the study.**
Timema monikensis, Timema tahoe, Timema genevieve	***Timema cristinae, Timema bartmani, Timema podura***	**Phylogenetic relationships within the genus *Timema* are clear. Sister sexual lineage of *Timema monikensis* is *Timema cristinae*, sister sexual lineage of *Timema tahoe* is *Timema bartmani* and sister sexual lineage of *Timema genevieve* is *Timema podura*. *Timema monikensis* could even be internal lineage of recent *Timema cristinae*** (Law & Crespi, 2002a, b). **All mentioned species are ecologically comparable.**

The majority of lineages of genus *Lasaea*	***Lasaea australis*, *Lasaea colmani***	**Only two diploid Australian lineages of genus *Lasaea*, *Lasaea australis* and *Lasaea colmani*, are sexual** (Ó Foighil & Smith, 1995; Ó Foighil & Thiriot-Quievreux, 1999). **But the asexual lineages of genus Lasaea almost certainly are not monophyletic and originated at least two times independently** (Thiriot-Quivreux, 1992; Ó Foighil & Smith, 1995; Taylor & Ó Foighil, 2000; Li et al., 2013). **Some of them are closer to *Lasaea australis*, whereas others to *Lasaea colmani*. Moreover, both sexual species probably do not have basal position within respective clades** (Taylor & Ó Foighil, 2000; Li et al., 2013). **This leaves us only with the option to compare all sexual with all asexual lineages of the genus. All mentioned lineages are ecologically comparable.**

Supplemental Materials and Methods: Details on determination of environmental heterogeneity

Biotic heterogeneity

We define biotically highly heterogeneous environments as those in which selective pressures affecting the offspring differ profoundly from those that previously affected their parents because of the coadaptation (or rather counter-adaptation) of interacting organisms. Thus, the most biotically heterogeneous environments are the habitats with a high degree of competition, predation, and parasitism. Biotic heterogeneity has both temporal (the coadaptation of interacting organisms) and spatial (e.g. the migration of the offspring to the areas with new competitors, predators, and parasites) dimensions. Changes in the biotic heterogeneity are essentially unpredictable, with the exception of some ecological cycles (e. g. host-predator or host-parasite cycles). In the latter case, environments with unpredictable changes were considered more biotically heterogeneous.

For example, the environment of organisms that live in tight association with other organisms is biotically very heterogeneous. This applies especially to predators and parasites that are forced to respond to the evolutionary counter-moves of their prey and hosts (Dawkins & Krebs, 1979). The more specific relationship with prey and hosts they have, the stronger the selective pressures of counter-adapting prey and hosts affect them (Dawkins & Krebs, 1979). Therefore, it is expected that organisms that use non-specific predatory strategies, e.g., filtering (especially if they filter both living organisms and dead organic matter), are under relatively weak selective pressure from their prey. Their environment is consequently biotically relatively homogenenous in this regard. On the other hand, the environment of organisms that are themselves under strong selective pressure of predators and parasites is highly biotically heterogeneous (Dawkins & Krebs, 1979). The environemnt of organisms that are not under strong selective pressures of predators and parasites for various reasons is biotically more homognenous in this regard (e.g. the environment of Darwinulidae, see Schön et al., 2009 or Bruvo et al., 2011). Another important component of environmental biotic heterogeneity is competition. The environments with complex ecosystems that are characterized by high a degree of competition, predation and parasitism among their inhabitants (e.g. ancient lakes, see Martens, 1998; Martens & Schön, 2000; Schön & Martens, 2004) are highly biotically heterogeneous for them. On the other hand, the environments with a low degree of competition, predation and parasitism (especially extreme habitats, e.g. the environments of extremely high temperatures, see Tobler, 2007, or, for photosynthetic organisms, poorly lit environments, see Farrar, 1978, 1998), are biotically very homogeneous for their inhabitants. The vast majority of environments on Earth are thus somewhat biotically heterogeneous. In spite of that, we can find important exceptions. This factor of environmental heterogeneity is considerably weakened especially in extreme, ephemeral and marginal habitats that cannot sustain complex ecosystems because of their extreme conditions, rapid unpredictable changes, low carrying capacity and/or insufficient energy sources (see e.g. Bell, 1982).

An important factor that affects the biotic heterogeneity of environment the organisms experience is the way of life practiced by aquatic organisms. On the average, lesser biotic heterogeneity is experienced by benthic (or sedentary) organisms in comparison with planktonic aquatic organisms. The reason is that the latter are subject to fast and effective transmission of parasites and pathogens, especially viruses (see e.g. Suttle et al., 1990; Bratbak et al., 1993; Fuhrman, 1999; Wommack & Colwell, 2000; Suttle, 2005, 2007), because of the character of their environment—mixing of water masses lead to frequent encounters of various individuals (Emiliani, 1993a, b). Crucial difference of the resulting risks for benthic and planktonic organisms was pointed out by Emiliani (1982; 1993a). Emiliani (1993a) documented that benthic representatives of Foraminifera have lower risk of extinction in comparison with planktonic ones. The average length of existence of their benthic species was 20 million years, whereas planktonic species lasted only about 7 million years. The most probable explanation of this pattern is higher susceptibility of planktonic organisms to extinction caused by lethal parasitic, especially viral, infections. This finding gave rise to the viral theory of background extinctions (Emiliani 1993a, b). Evidence for the lower risks arising for benthic organisms from parasites and pathogens was also supported by other ecological studies. For example, Filippini et al. (2006) observed lower prevalence of individuals infected by viruses and consequent mortality among benthic bacteria (~0.03 %) in comparison with bacteria from water column (~6 %). Moreover, this pattern held despite much larger abundance of viruses in the sediment of studied temperate lake. Fisher et al. (2003) and Bettarel et al. (2006) came to very similar conclusions on the basis of studies of temperate oxbow lake and freshwater habitats in tropical Africa, respectively (but see Danovaro et al., 2008 for somewhat contrasting results from marine benthic sediment). Putting aside the limitations of parasite and pathogen transmission among benthic organisms, the protection of benthic organisms against viruses might be further enhanced by the adsorption of viruses into organic and inorganic particles of sediment and the aggregation of benthic organisms (Filippini et al. 2006; Fisher et al., 2003). Whereas the extinction of whole species due to viral infection (eventually infection by another parasite or pathogen, e.g. fungus) is possible only under very limited conditions (see e.g. Buckwold, 1994, or de Castro & Bolker, 2005), local extinctions caused by pathogen or parasitic infections are probably quite common (Emiliani, 1982, 1993a; de Castro & Bolker 2005). The planktonic way of life thus probably considerably increases the selective pressures of parasites and pathogens and consequently the biotic heterogeneity of the environment.

The argument for lower biotic heterogeneity of benthic (or sedentary) organisms is possible to extend also to organisms that inhabit soil. From the viewpoint of the viral theory of background extinctions (Emiliani, 1993a, b), soil represents an environment that considerably impedes the spread of pathogens and parasites. Interactions with parasites and pathogens are very limited both in intensity and frequency due to the tortuous, i.e., multidimensional, character of soil matrix—it is best described as semi-discontinuous network of pores filled with air and/or water, or water films surrounding solid particles (Lavelle & Spain, 2003; for more information about the character of soil environment see also Wallwork, 1970; Coleman et al., 2004, or Paul, 2007). These features of soil matrix limit both the passive spread of parasites and pathogens and the frequency of encounters among their transmitters and organisms in general. The tortuous character of soil environments was stressed as a factor that limits the passive spread of viruses in benthic sediment by Fisher et al. (2003), whereas Murphy & Tate (1996) emphasized its limitations on the spread of bacteria. These observations are in agreement with Drake et al. (1998), who observed a negative correlation between the concentration of viral particles and sediment grain size. The sieving effect of the soil for organisms of various sizes is also commented by Paul (2007). Moreover, the tortuous character of soil impedes also active dispersion of organisms, e.g. when searching for prey (Elliott et al., 1980). Only a few larger organisms are able to effectively move larger distances within soil or even create their own habitats; movements of most organisms are locally constrained (Lavelle & Spain, 2003). Direct encounters between organisms, even organisms of the same species, are thus relatively infrequent. This leads, together with the limited spread of pheromones (Karasawa & Hijii, 2008), for example, to frequent transitions to indirect fertilisation with the help of deposited spermatophores (see e.g. Wallwork, 1970, or Lavelle & Spain, 2003). The pattern of spatial autocorrelation of genetic lineages in soil communities, for example in rotifers (Robeson et al., 2011), further supports the limited dispersal abilities of soil organisms. The genetic diversity of various Bdelloidea lineages in soil is correlated only on small spatial scales (up to 54-133 m). Operational taxonomic units identified by Robeson et al. (2011) almost did not overlap above this distance. Habitats that distanced only tens to hundreds of meters were thus inhabited overwhelmingly by separate genetic lineages. Moreover, rotifer communities differed to a certain degree even in the smallest investigated distance of 16 cm (Robeson et al., 2011)[1].

Taken together, the tortuous character of the soil affects all soil organisms at various scales not only in terms of the reduced spread of parasites and pathogens, but also lower frequencies of encounters with predators and competitors. This leads to an overall reduction of biotic pressures in soil, which is further supported by the striking evolutionary stasis of many lineages of soil inhabiting organisms (Pilato, 1979). Moreover, species richness and population sizes, including parasites, predators and competitors, markedly decreases with the depth of soil horizon (Lavelle & Spain, 2003; Paul, 2007). Deep soil horizons are therefore even more abiotically homogeneous. The specific character of soil environment does not imply its general spatial homogeneity. On the contrary, soil is often spatially heterogeneous, especially on a larger scale (see e.g. Lavelle & Spain, 2003; Coleman et al., 2004, or Paul, 2007). It is the tortuous and multidimensional character of soil matrix that reduces biotic pressures affecting its inhabitants and makes this environment biotically very homogeneous.

The biotic heterogeneity of the environment the organisms experience might be reduced by the presence of durable resting stages. Organisms may get rid of parasites and pathogens, survive unfavourable environmental conditions, or colonize new habitats with naïve parasites, predators, pathogens and competitors in these stages (as do, for example, Bdelloidea—see Wilson, 2011). The geographical trend of decreasing biotic heterogeneity with increasing latitude might be expected on a global scale. Species diversity and ecosystem complexity decrease with distance from equator (Tokeshi, 1999). These events are coupled with a decreasing intensity

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[1] High genetic diversity of Bdelloidea in gene cox1 is not very surprising in the light of severe DNA breaks that originate during anhydrobiosis, following repairs of these breaks and consequent intensive horizontal gene transfer (see e.g. Gladyshev et al., 2008).

of parasitization, abundance, prevalence and a relative diversity of parasites (Rohde, 1986; Rohde & Heap, 1998). An analogous trend of decreasing biotic heterogeneity with increasing depth might be expected in deeper parts of the water column for the same reasons (see e.g. Etter et al., 2005).

Abiotic heterogeneity

Abiotically highly heterogeneous environments are defined as those that are highly variable regarding changes of abiotic factors. They are diverse, unstable, and have unequally distributed resources. Again, the abiotic heterogeneity of the environment has both spatial (in the sense of variability) and temporal (in the sense of instability) dimensions. The offspring thus usually inhabit an environment different from that of their parents due to their dispersal in time and/or space. Changes in the abiotic environment could be predictable (e.g. cyclical) or unpredictable, and their intensity and frequency vary on different timescales. We are interested in ecological timescales in this study so we consider short-term unpredictably changing environments as the most abiotically heterogeneous.

Temporally and spatially highly changeable ephemeral and marginal habitats are especially abiotically heterogeneous environments (see e.g. Pejler, 1995). However, most of the surface terrestrial habitats are considerably abiotically heterogeneous. On the contrary, sheltered habitats such as caves, ground water reservoirs or soil environment are greatly abiotically homogenenous. Such environments protect their inhabitants from solar radiation and buffer short-term fluctuations in outer environment (e.g. changes of temperature and humidity), protecting their inhabitants from the direct impacts of such changes (Wallwork, 1970; Farrar, 1978, 1990, 1998; Krivolutsky & Druk, 1986; Lavelle & Spain, 2003; Devetter & Scholl, 2014). Most changes in soil matrix are much slower in comparison with surface habitats (Lavelle & Spain, 2003). The abiotic homogeneity of soil environment further increases with the depth of the soil horizon. For example, there is a specific depth of soil horizon in each geographical region under which the temperature is perienally stable, depending on its latitude, altitude and other climatic factors (Wallwork, 1970; Lavelle & Spain, 2003; Coleman et al., 2004; Paul, 2007). The buffering effect of soil on moisture fluctuations also increases with depth (see e.g. Quesada et al., 2004). Moreover, soils of certain biomes (especially forest soils) are temporally abiotically more homogeneous than soils of other biomes (see e.g. Siepel, 1994, 1996).

Regarding aquatic environments, freshwater habitats and coastal areas are the most abiotically heterogeneous (Sheldon, 1996). The decrease of abiotic heterogeneity with increasing depth is also expected—water masses buffer surface environmental changes in a similar way to soil (see e.g. Etter et al., 2005). Certain extreme environments that are temporally stable (e.g. hot springs or subsurface cavities) are also very abiotically homogeneous (Bell, 1982), but this does not apply to all environments referred to as extreme.

In a similar way to the biotic heterogeneity of the environment, also the abiotic one might be reduced in the populations of organisms producing durable resting stages. Such an adaptation enables them to survive unfavourable fluctuations of an abiotic environment and promotes colonization of new habitats (see e.g. Wilson, 2011). On the other hand, mobility probably does not strongly affect the abiotic environmental heterogeneity that the organisms experience. Mobile organisms might hypothetically experience more different abiotic conditions in their life, but they can also easily stick with those most suitable for them. The geographical trend of increasing abiotic heterogeneity with increasing latitude and altitude might be expected to occur on global scale (Hörandl, 2006, 2009; Vrijenhoek & Parker, 2009). However, it is noteworthy that such a trend might be countered by an opposite trend of the decreasing biotic heterogeneity mentioned above in its effects on sexual and asexual species (and *vice versa*). All the expectations mentioned above need not apply absolutely, but may serve as useful leads in judging the environmental heterogeneity of various organisms if their peculiarities are taken into account.

Supplemental review of AA ecology

Bdelloidea

Bdelloidea is clade of hundreds of µm sized rotifers associated with semi-terrestrial, freshwater and soil environments (Ricci & Balsamo, 2000; Welch et al., 2009). Members of the ancient asexual group Bdelloidea inhabit most freshwater surface habitats, but are sometimes found also in brackish water and marginally in seawater (De Smet, 2002). Among freshwater environments, Bdelloidea dominate in biotically homogeneous marginal habitats with a reduced number of parasites, predators and competitors in contrast to its sexual control Monogononta (Ricci, 1987; Pejler, 1995; Ricci & Balsamo, 2000; Welch et al., 2009). They are exclusively benthic or sedentary (Koste & Shiel, 1986; Ricci & Balsamo, 2000), which indicates reduced biotic heterogeneity in contrast with sexual control. Monogononta are not only sedentary, but also obligately or facultatively planktonic and several of their species are clearly marine (Pejler, 1995). Concerning the biotically and abiotically homogeneous soil environment, Bdelloidea far outnumbers their sexual control there (Pejler, 1995). Bdelloidea overwhelmingly dominate among soil rotifers and rotifers associated with mosses (Bryophyta) and lichens (Pejler, 1995; Scholl & Devetter, 2013; Devetter & Scholl, 2014), reaching up to 95 % prevalence (Donner, 1975). Moreover, Bdelloidea are almost exclusive among rotifers in high mountain soil (at least in Himalayas—Devetter M., pers. comm. 2015). Abiotically homogeneous groundwater reservoirs are inhabited both by Monogononta and Bdelloidea. However, these habitats are poorly explored and observed species were probably transported there recently (Pejler, 1995). Bdelloidea are almost completely absent from biotically heterogeneous ancient lakes (e.g. Baikal) with complex ecosystems and intensive biotic interactions (predators, parasites and competitors). Sexual Monogononta overwhelmingly dominates here (Martens & Schön, 2000; Schön & Martens, 2004).

Anhydrobiosis, i.e. drying into the state of durable resting stages, is the key ability of Bdelloidea from the ecological viewpoint. It enables Bdelloidea to avoid unpredictable and unfavourable conditions in its surrounding environment. Bdelloidea often inhabit objectively abiotically very heterogeneous environments, but activate only under the most suitable conditions (Pilato, 1979; Ricci, 2001). Anhydrobiosis thus makes them experience only favourable conditions and makes their environment subjectively highly abiotically homogeneous. Moreover, anhydrobiosis enables them to get rid of parasites (Wilson & Sherman, 2010; Wilson, 2011) and effectively disperse in space and time (Caceres & Soluk, 2002), which may also reduce the biotic heterogeneity of environment they experience. Anhydrobiosis is also tightly connected to other specific characteristics of Bdelloidea—exceptionally intensive horizontal gene transfer (Gladyshev, Meselson & Arkhipova, 2008; Debortoli et al., 2016), frequent repairs of DNA double-strand breaks and exceptional resistance to radiation (Gladyshev & Meselson, 2008) and starving (Ricci & Perletti, 2006). Intensive horizontal gene transfer is probably the reason for the relatively large genetic differences among clades of soil Bdelloidea that inhabit environments that distance from tens to hundreds of meters, as observed by Robeson et al. (2011). This alternative mode of genetic exchange was also proposed as an explanation for their ancient asexuality, substituting for their ability of genetic exchange during sexual processes (Boschetti et al., 2011; Gladyshev et al., 2008; Debortoli et al., 2016; Schwander, 2016)[2]. However, Bdelloidea are extremely phenotypically conservative (Pilato, 1979) despite their intensive horizontal gene transfers, which supports the primacy of homogeneous environment in the long-term maintenance of their asexuality. Sexual Monogononta does not have the ability of anhydrobiosis. They only produce mictic eggs at the end of the season, durable resting stages that serve for the survival of predictable periods of unfavourable conditions (Ricci, 2001). The character of the environment that they subjectively experience is thus much more biotically and abiotically heterogeneous.

It is noteworthy that Bdelloidea are ecologically more successful in thermally extreme environments. Both Monogononta and Bdelloidea are found in polar regions (Dartnall, 1983; Pejler, 1995; Sohlenius & Bostrom, 2005; Jungblut et al., 2012). However, Bdelloidea—especially *Philodina gregaria*—reaches much higher population densities and form growths sized up to several m^2 in these habitats (Dartnall, 1983; Pejler, 1995). Bdelloidea also reach much larger abundances than Monogononta in polar habitats (Janiec, 1996). These habitats are biotically very homogeneous because of reduced biotic interactions. They are also experienced as

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[2] The role of horizontal gene transfer in bdelloid rotifers as a substitution for sexual processes remains intensively discussed. On the one hand, it was proposed that bdelloids in fact experience rare sex (Signorovitch et al., 2015; 2016), but on the other that the observed genetic exchange is best explained by intensive horizontal gene transfer (Debortoli et al., 2016; Flot et al., 2016). Due to the strong evidence supporting the absence of amfimixis in Bdelloidea (see table S1), we incline to think that Bdelloidea do not experience standard sexual processes (nevertheless, see Signorovitch et al., 2015; 2016; Debortoli et al., 2016; Flot et al., 2016). In either case, the rate of horizontal gene transfer in bdelloid rotifers is extraordinary high and probably tightly connected to their long-term survival in asexual state (Schwander, 2016).

very abiotically homogeneous by Bdelloidea because of their ability to survive adverse conditions in anhydrobiotic state. Bdelloidea are also more successful in comparison with their sexual control at high temperatures. Issel (1900, 1901) observed *Philodina roseola* in Italian hot springs at temperatures up to 46 °C. He concluded that *Philodina roseola* is specialized to high temperatures and dominates over sparse members of Monogononta above 40 °C. Pax and Wulfert (1941) reached similar conclusions in their research of central European hot springs. This pattern is further supported by environmental sequencing of hot springs in Alaska (McDermott & Skorupa, 2011). Despite the limitations of this study—for example, the authors could not distinguish the sequences of active living individuals from sequences of inactive individuals, dead specimens or contamination—the sequences of Bdelloidea, specifically *Philodinidae*, overwhelmingly dominated in springs with temperatures above 40 °C. The habitats of hot springs are abiotically stable and thus abiotically very homogeneous. Moreover, the number of competitors, predators and parasites decreases at high temperatures, which makes these environments biotically very homogeneous.

Bdelloidea and Monogononta predominantly feed by filtering surrounding water for small organic particles. Rarely, some sedentary representatives graze nutrients from nearby surfaces or drill through algal cell walls and suck its cytoplasm. However, there are no active predators among Bdelloidea in contrast to Monogononta (Ricci & Balsamo, 2000). The only single exception seems to be *Abrotrocha carnivora* (Ricci et al., 2001). None of two compared groups comprise parasites.

Taken together, Bdelloidea dominate over their sexual control in marginal habitats with reduced biotic heterogeneity. Anhydrobiosis shields its representatives from unfavourable conditions of their abiotic environment and consequent selection. Bdelloidea thus experience even abiotically homogeneous environment. Moreover, anhydrobiosis protects them to a certain degree even from the unfavourable consequences of intensive biotic pressures—it enables Bdelloidea to get rid of parasites and escape parasites, predators and competitors in time and space. Anhydrobiosis thus reduces even the experienced biotic heterogeneity of their environment. Bdelloidea dominate over their sexual control among rotifers inhabiting biotically and abiotically homogeneous soil environment. Bdelloidea are also ecologically very successful in biotically homogeneous polar regions with a low amount of biotic interactions (an environment which is for them also abiotically homogeneous due to anhydrobiosis) and abiotically stable hot springs with reduced biotic pressures (abiotically and biotically homogeneous environments). Bdelloidea thus predominate over their sexual control even in objectively homogeneous environments. Cyclically sexual Monogononta dominate over Bdelloidea in water column and have numerous planktonic and sea representatives. Some of their species are predatory and thus experience stronger biotic pressures. They do not have the ability to undergo anhydrobiosis and thus live in subjectively much more heterogeneous environment than Bdelloidea. Monogononta also overwhelmingly prevail over Bdelloidea in ancient lakes with intensive biotic interactions. In conclusion, Bdelloidea are associated with biotically and abiotically more homogeneous environments than their sexual control Monogononta.

Darwinuloidea

Darwinulidae is the only extant member of superfamily Darwinuloidea. It is a group of hundreds of µm sized ostracods (Schön et al., 2009). Darwinulidae are present in most aquatic habitats including marine (see e.g. Martens et al., 1998a). In a similar way to Bdelloidea, Darwinulidae are also predominantly associated with biotically homogeneous marginal and semi-terrestrial habitats or springs and biotically and abiotically homogeneous interstitial and soil (Schön et al., 1998; Pinto et al., 2005; Pieri et al. 2009; Schön et al., 2009). However, the sexual control of Darwinulidae, Cypridoidea, is also present in the same environments and Darwinulidae does not seem to prevail there over its sexual control. Some representatives of Cypridoidea are planktonic (Pokorný, 1965), whereas all representatives of Bdelloidea are exclusively benthic or sedentary (Schön et al. 1998, 2009; Pinto et al. 2005; Pieri et al. 2009). This indicates a reduced abiotic heterogeneity of their environment.

Darwinulidae are able to survive unfavourable conditions (drought, low temperatures etc.) in an inactive state of torpor (Carbonel et al., 1988). This ability may be superficially analogical to anhydrobiosis of Bdelloidea in its ecological consequences, but does not enable Darwinulidae to survive such severe conditions. In any case, the environment is also experienced as subjectively abiotically homogeneous by Darwinulidae at least to some degree. The ability to undergo torpor may also outweigh the absence of durable eggs that are present in the sexual control (Horne, 1993). However, numerous representatives of Cypridoidea are also capable of torpor and this ability is thus not exclusive to AA Darwinulidae in contrast to Bdelloidea-Monogononta (Delorme & Donald, 1969;

Carbonel et al., 1988; Retrum et al., 2011). Moreover, even representatives unable to enter a state of torpor are able to survive short periods of drought (Retrum et al., 2011). A Darwinulidae-specific brooding pouch is also an important part of resistance to unfavourable conditions of biotic and abiotic environments. It protects offspring from fluctuations of abiotic environmental factors and predators and also facilitates the dispersal abilities of Darwinulidae (Martens, 1998). Its presence may decrease the experienced biotic and abiotic heterogeneity of the environment.

Darwinulidae are not predominantly associated with permanent bodies of water. However, the individuals that inhabit them prefer hypoxic depths with lower biotic pressures (Rossi et al., 2002; Smith et al., 2006; Schön et al., 2009). Such depths are also optimal for dispersion with the help of water birds, but the depth preference of Darwinulidae does not seem to be selected primarily for this reason. Despite the fact that Darwinulidae have numerous preadaptations hypothetically promoting its dispersal (see e.g. Delorme & Donald, 1969; Martens, 1998; Frisch et al., 2007; Retrum et al., 2011), they are probably not good colonizers (Malmqvist et al., 1997; Martens et al., 2008b). Another explanation, for example, the absence of predators, predators and competitors in hypoxic areas and consequently reduced biotic heterogeneity, seems more plausible. Darwinulidae are also nearly absent from ancient lakes with strong biotic pressures, which are dominated by sexual ostracods (Schön & Martens, 2004). A similar pattern also applies to groundwater (Schön & Martens, 2004; Martens et al., 2008a). These environments are highly biotically heterogeneous.

Darwinulidae are not more prevalent or ecologically successful in thermally extreme environments in comparison with their sexual control. The lower limits of their activity lie around 0 °C, which is similar to Cypridoidea (McLay, 1978; Tudorancea et al., 1979; Külköylüoğlu & Vinyard, 2000; Bunbury & Gajewski, 2009). The upper limits of their activity are inferior to those of Cypridoidea. Some species of Cypridoidea are specialized to high temperatures and activate even at 54 °C (Külköylüoğlu et al., 2003). Other Cypridoidea representatives were observed as ecologically successful at temperatures around 50 °C (Moniez, 1893; Brues, 1932; Klie, 1939; Jana & Sarkar, 1971; Wickstrom & Castenholz, 1985). Darwinulidae only rarely activate at temperatures above 35 °C (Brues, 1932; Reeves et al., 2007) and their upper thermal limit of activity lies around 40-50 °C (Menzel, 1923; Ponyi, 1992). They are thus not associated with thermally more extreme biotically or abiotically homogeneous environments in comparison with their sexual control.

Another characteristic of Darwinulidae is that they are highly resilient to starvation (Rossi et al., 2002) and only rarely predated (Ranta, 1979). Moreover, ostracods in general are rarely and weakly parasitized (Schön et al., 2009; Bruvo et al., 2011), which may be an effective preadaptation to their frequent transitions to asexuality—young asexual lineages are common also in Cypridoidea. All of this indicates that they experience reduced biotic heterogeneity of their environment. The pattern of geographical parthenogenesis, i.e. increasing number of asexual lineages with latitude and altitude, is also often commented in ostracods. The distribution in higher latitudes and altitudes is associated with increased abiotic heterogeneity and decreased biotic heterogeneity. However, this pattern does not have general applicability in the compared taxa (Bell, 1982: 265-266; Schwander & Crespi, 2009). It applies only to certain species of Cyprididae that consist of sexual and asexual lineages (Horne et al., 1998).

Environmental correlates of AA Darwinulidae and its sexual control Cypridoidea are similar to Bdelloidea-Monogononta, but their differences are not nearly as distinct. Biotically and abiotically very homogeneous environments are inhabited both by the AA group and its sexual control in many ways. There are only few absolute differences between the compared groups. One reason for this "fogginess" might be the large disproportion in the number of species in the two compared clades. Sexual Cypridoidea comprise more than 1500 described species, whereas Darwinulidae are comprised by only about 40 (Martens et al., 1998a, b; Rossetti et al., 2011). Another possible reason is frequent transition to asexuality in certain species of Cypridoidea and consequent presence of many young asexual lineages (Martens, 1998). Such young asexual lineages may have transient advantage over sexual species in numerous environments that are also associated with the AA lineage (Martens, 1998).

Taken together, Darwinulidae tend to be associated with biotically homogeneous marginal habitats in a similar way to Bdelloidea-Monogononta. Moreover, they also experience such habitats as subjectively abiotically homogeneous because of their ability to undergo torpor. However, the same environments are equally inhabited by the sexual control Cypridoidea that is also capable of torpor. Darwinulidae thus does not seem to be associated with abiotically more homogeneous environments than their sexual control. The same pattern applies to the association with abiotically and biotically homogeneous soil habitats or the absence of predatory and parasitic lifestyle and lower overall parasitization that mark more biotically homogeneous environment—it is characteristic for both compared groups. However, Darwinulidae are exclusively benthic or sessile in contrast to their sexual control, which is associated with a reduction of biotic heterogeneity. They are also nearly absent from the biotically complex environments of ancient lakes and are sparse in groundwater reservoirs that are both biotically heterogeneous. Species of Darwinulidae that inhabit stable water bodies such as lakes and rivers prefer hypoxic depths with reduced biotic stresses. Moreover, Darwinulidae are only under a weak pressure of predators and are resilient to starvation. All of that is associated with reduced biotic heterogeneity. In conclusion, ostracods are associated with markedly homogeneous environments in general. Darwinulidae in particular are associated with biotically more homogeneous environments in comparison with their sexual control. However, there is no clear difference in the abiotic heterogeneity of the environments Darwinulidae and their sexual control are associated with.

Oribatidae

Oribatidae is a diverse group of hundreds of μm sized mites (Norton & Behan-Pelletier, 2009). AA representatives of mites from the clade Oribatidae are predominantly associated with soil in contrast to their sexual controls. Moreover, their proportion increases with the depth of the soil horizon (Krivolutsky & Druk, 1986; Norton & Palmer, 1991; Karasawa & Hijii, 2008; Maraun et al., 2009; Devetter & Scholl, 2014). Soil is a biotically and abiotically more homogeneous environment in comparison with surface habitats. The upper layers of soil are abiotically relatively more changeable and characterized by more complex biotic interactions; biotic and abiotic heterogeneity further decreases with the depth of the soil horizon. This indicates an association of AA Oribatidae with biotically and abiotically homogeneous environments. On the other hand, sexual lineages of Oribatidae predominate in biotically and abiotically more heterogeneous arboreal habitats (Karasawa & Hijii, 2008; Maraun et al., 2009). Beyond that, AA representatives of Oribatidae are preferentially associated with abiotically more stable forest soils rather than changeable grassland soils (Krivolutsky & Druk, 1986; Siepel, 1994; but see also Devetter & Scholl, 2014 that proved stronger effect of seasonality in contrast to substrate and vegetation cover). There are almost no typical parasites and predators among AA Oribatidae, which may indicate a lower biotic heterogeneity of their environment. They are saprophages, fungivores, or feed on algae and microorganisms. However, the same applies also to their sexual controls (Norton & Behan-Pelletier, 2009).

In the context of abovementioned characteristics, it is rather surprising that AA Oribatidae were not proven to be predominantly associated with biotically more homogeneous environments characterized by a reduced number of competitors and predators (Cianciolo & Norton, 2006). However, the study of Cianciolo and Norton (2006) might examine too narrow spectrum of their predators and parasites. Other experiments proved that AA representatives of Oribatidae are superior to sexual ones in abiotically homogenenous environment with unlimited unstructured resources. Sexual Oribatidae were more succesfull in the presence of structured resources (Domes et al., 2007c; Maraun et al., 2012).

The possible geographical parthenogenesis of Oribatidae, i.e. a higher proportion of asexual lineages in higher latitudes and altitudes characterized by higher abiotic heterogeneity and lesser biotic heterogeneity, remains questionable. Some studies supported this pattern (Behan-Pelletier, 1997), but other evidence is very unclear (Norton & Palmer, 1991; Cianciolo & Norton, 2006).

Taken together, AA lineages of Oribatidae are predominantly associated with biotically and abiotically homogeneous soil environment in contrast to their sexual controls. Moreover, the proportion of AA lineages increases with the depth of the soil horizon that is associated with further reduction of biotic and abiotic heterogeneity. They are less prevalent in arboreal environments that are more abiotically changeable and characterized by stronger biotic pressures, i.e. abiotically and biotically more heterogeneous. AA Oribatidae are also preferentially associated with abiotically stable forest soils in contrast to more changeable grassland soils. There are no typical predators and parasites among AA Oribatidae, but the same also applies to their sexual controls. A direct association with more biotically homogeneous environments in soil remains questionable. However, they are more successful in environments with unstructured resources in contrast to sexual representatives. The geographical parthenogenesis of Oribatidae, potentially associated with increase of abiotic heterogeneity and decrease of biotic heterogeneity with latitude and altitude, remains an open question. In conclusion, AA Oribatidae seems to be affected mainly by abiotic conditions of environment, but generally inhabit both biotically and abiotically more homogeneous environments in comparison with their sexual controls.

Other ancient asexual mites

Endeostigmata is a group of hundreds of μm sized mites predominantly associated with soil and especially extreme soil habitats—deep soil or sand horizons, microbial crusts, extremely salty habitats, seashores and desert soils (Walter, 2009). Such habitats are expected to be biotically more homogeneous. AA Endeostigmata tend to be associated with deep soil horizons in contrast to their sexual controls. All of their sexual controls are associated with abiotically and biotically more heterogenenous environments, especially abiotically relatively changeable upper parts of the soil with more biotic interactions. The only exception from this rule is the clade comprising of Grandjeanicidae and Oechserchestidae that do not exhibit any differences in heterogeneity of their environment in comparison with their sexual control (Norton et al., 1993; Walter, 2001, 2009; Neher et al., 2009; Norton & Behan-Pelletier, 2009; Oconnor, 2009; Darby et al., 2011). A predatory lifestyle is very rare among AA Endeostigmata and they are never parasitic. They are mostly saprotrophs, or feed on fungi and microorganisms, which makes their environment less biotically heterogeneous. However, this is also true for their sexual controls among Endeostigmata (Walter, 2001, 2009; Neher et al., 2009). A group consisting of genera *Alicorhagia* and *Stigmalychus* is an exception from this pattern, because it is much less phenotypically variable than any possible sexual control. Some of these controls are large lineages outside of Endeostigmata that comprise even typical predators and parasites (Norton et al., 1993; Walter, 2001, 2009; Neher et al., 2009; Norton & Behan-Pelletier, 2009; Oconnor, 2009; Darby et al., 2011). Taken together, their ecological patterns are similar to those of Oribatidae. They are just even less explored.

Trombidiformes is another diverse clade of hundreds of μm sized mites (Walter et al., 2009). Ecological patterns of AA lineages among Trombidiformes are analogical to those of Oribatidae and Endeostigmata (Kethley, 1989; Bochkov & Walter, 2007; Neher et al., 2009; Walter et al., 2009; Darby et al., 2011). However, they are also poorly explored. These AA mites are also predominately associated with biotically and abiotically homogeneous deep soil horizons and are not typically predators and parasites, which reduces the biotic heterogeneity of their environment (Norton et al., 1993; Neher et al., 2009; Walter et al., 2009; Darby et al., 2011). Their sexual controls from clade Prostigmata (and Sphaerolychidae in case of Lordalycidae), both alone and in any combination (their phylogenetic position is unclear), are much more phenotypically disparate and comprise even typical predators and parasites (Neher et al., 2009; Norton et al., 1993; Walter et al., 2009; Darby et al., 2011).

Taken together, all abovementioned mite groups are poorly explored. However, if we can judge anything from the current knowledge of their ecology, it is that their AA lineages seem to be associated with biotically and abiotically more homogeneous environments. They are associated with soil and, in contrast to their sexual controls, especially deep soil horizons. Moreover, Trombidiformes, as well as *Alicorhagia* and *Stigmalychus*, are much less phenotypically variable than any of their sexual controls that comprise even predators and parasites and inhabit more biotically and abiotically heterogeneous environments. With the exception of Oehserchestidae that doesn’t inhabit environments of different heterogeneity than their sexual control, we can conclude that AA mite lineages are always associated with more biotically and abiotically homogeneous environments than their sexual controls.

Vittaria

Vittaria appalachiana is an mm sized fern (Polypodiophyta) from the family Vittariaceae that forms growths up to several m^2 large (Farrar, 1978; Farrar & Mickel, 1991). It is unique among ferns by abandoning the stage of sexual gametophyte and surviving as purely an asexual sporophyte. *Vittaria appalachiana* is rather a group of related asexual lineages as opposed to a single species—individual populations are genetically and phenotypically variable (Farrar, 1978, 1985, 1990). *Vittaria appalachiana* is associated almost exclusively with caves, crevices and rock excesses that buffer fluctuations of outer temperature and humidity (Farrar, 1978, 1985, 1990). Populations of *Vittaria appalachiana* thus inhabit geologically and ecologically stable habitats (Farrar, 1998) that are characterized by low abiotic heterogeneity. Moreover, extremely low levels of light in its habitats lead to a strong reduction of interspecific competition (Farrar, 1978, 1998) and lower biotic heterogeneity. *Vittaria appalachiana* also inhabit higher latitudes in comparison with any proposed sexual control (Farrar, 1998, 1978; Farrar & Mickel, 1991), which could lead to a reduction of biotic heterogeneity. A possible co-occurring increase of abiotic heterogeneity with latitude probably does not affect *Vittaria appalachiana* strongly because of its buffering habitats. The association of *Vittaria appalachiana* with biotically homogeneous environments is further supported by the fact that individual plants are highly susceptible to parasitization and competition (as well as antibiotics and sterilisation), as was observed during attempts to grow them in a laboratory (Caponetti et al., 1982). Its sexual controls do not exhibit these characteristics. Sporophytes of all proposed sexual controls grow epiphytically on decaying wood or trees in lower latitudes. Their habitats are thus more exposed to abiotic conditions of environment, biotically and abiotically more heterogeneous (Farrar, 1978, 1990; Farrar & Mickel, 1991).

Taken together, caves and rock overhangs inhabited by *Vittaria appalachiana* in contrast to all proposed sexual controls are geologically and ecologically stable, maintain stable level of humidity and protect their inhabitants from fluctuations of temperature. These habitats are thus abiotically very homogeneous. Extremely low levels of light in these habitats also strongly reduce any interspecific competition. This leads, as well as higher latitudes inhabited by *Vittaria appalachiana*, to lower biotic heterogeneity of its environment in comparison with any sexual control. Moreover, the individuals of *Vittaria appalachiana* are highly susceptible to infections and are not good competitors. This also points to their association with biotically homogeneous environments. In conclusion, *Vittaria appalachiana* is associated with more biotically and abiotically homogeneous environment than any of its proposed sexual controls.

Timema

Timema is a genus of cm sized herbivorous phasmatodean (Phasmatodea) insects that inhabit chaparral vegetation of western pars of North America (Vickery, 1993; Sandoval et al., 1998). Sexual, young sexual and AA lineages of the phasmatodean (Phasmatodea) genus *Timema* do not differ much in their ecology. Two of three AA species have narrower food spectra in comparison with their sexual controls. This could hypothetically lead to decreased competition and consequently a biotically more homogeneous environment. However, a third AA species, *Timema tahoe*, share the same host plant as its sexual control *Timema bartmani* (Law & Crespi, 2002b). None of the AA species are more specialized in comparison with their sexual control. In fact, they are markedly similar in terms of their phenotype (Sandoval et al., 1998). The areas of AA *Timema* species are usually geographically separated from areas of other members of the genera, mostly by a great distance (Sandoval et al., 1998; Law & Crespi, 2002b). This may lead to decreased interspecific competition with other members of the genera (especially species with the same or overlapping food niche) and consequentially a decrease of the biotic heterogeneity of their environment. However, the areas of AA *Timema monikensis* and its sexual control *Timema chumash* overlap (Law & Crespi, 2002a), casting doubt on this possibility. On the other hand, young asexual species of the genera usually border and partially overlap their areas with sexual species of *Timema*, including their sister species (Law & Crespi, 2002b). Young asexual species of *Timema* also inhabit higher latitudes in comparison with their sexual relatives, which may indicate abiotically more heterogeneous but biotically more homogeneous environment. However, this pattern does not apply to AA species of *Timema* (Law & Crespi 2002a, b). Two of three AA species have markedly northern areas in comparison with their sexual controls. However, other species of *Timema*, including sexual ones, are distributed into even higher latitudes (Law & Crespi, 2002b).

Taken together, it doesn’t seem that the environment inhabited by AA members of *Timema* is biotically or abiotically more homogeneous or heterogeneous in comparison with their sexual controls. Some indices, e.g. the separation of areas populated by AA members of the genera from areas populated by other members, point to reduced interspecific competition and possibly a reduced biotic heterogeneity of their environment. The distribution of AA timemas in higher latitudes in comparison with sexual controls may have similar consequences. However, possible indices of differences among the environmental heterogeneity of AA members of *Timema* and their sexual controls are highly unclear. In conclusion, available evidence is insufficient to identify any consistent differences in biotic and abiotic heterogeneity of the environment of AA members of *Timema* and their sexual controls.

Lasaea

Lasaea is a genus of mm sized intertidal bivalves (Bivalvia) (Morton et al., 1957). Its AA representatives have global distribution, whereas sexual controls are limited only to the shores of Australia and Tasmania (Ó Foighil & Smith, 1995; Ó Foighil & Thiriot-Quievreux, 1999; Taylor & Foighil, 2000). AA representatives of *Lasaea* are thus distributed to higher latitudes with hypothetically a reduced biotic heterogeneity and an increased abiotic heterogeneity. However, they are present also in lower latitudes. The main reason for this geographical pattern is thus probably not the hypothetical difference in environmental heterogeneity, but the excellent dispersal ability of directly developing AA members of *Lasaea* (Ó Foighil, 1989). However, one of two sexual lineages of this genus, *Lasaea colmani*, also has direct development (Ó Foighil & Smith, 1995). It is thus difficult to make any conclusions on the basis of the association between their ancient asexuality with their direct development.

Lasaea is not associated with environments of a distinctly homogeneous character. It is associated with areas of tidal zone between the mean high water spring and low water spring tides. Its individuals are associated especially with shallow crevices and shaded stone recesses, empty barnacles and tufts of tidal vegetation (Morton et al., 1957). This boundary ecosystem is abiotically rather changeable, which may lead to decreased competition, predation and parasitization. However, *Lasaea* do not greatly experience reduced biotic pressures. Its individuals are associated with numerous marine plants, isopods (Isopoda), springtails (Collembola), mites (Acari), beetles (Coleoptera), pseudoscorpions (Pseudoscorpiones) and gastropods (Gastropoda). They are also accompanied by other bivalves in the lower parts of tidal zone (Morton et al., 1957). Amenzalous filamentous cyanobacteria and green filamentous algae (e.g. *Entocladia*) often grow on their shells and erode them (Morton et al., 1957). Species of genus *Lasaea* feed by filtering detritus and are not typical predators and parasites. However, these characteristics applies both to their AA and sexual lineages (Morton et al., 1957).

It is noteworthy that both AA and sexual lineages of *Lasaea* are not able to breath atmospheric oxygen in contrast to numerous tidal invertebrates. They tightly close their shells in unfavourable conditions (e.g. drought) and become inactive. Individuals of *Lasaea* are able to survive up to several days in this inactive state (according to Morton et al., 1957, up to 12 days). This ability primarily serves for their survival in the changeable conditions of tidal zone. However, it may also enable *Lasaea* to activate only under favourable conditions and consequently make its environment subjectively more homogeneous. Thus, it may be a preadaptation analogical to the anhydrobiosis of Bdelloidea or the torpor of Darwinulidae. However, thorough exploration of the hypothetical differences between AA and sexual lineages of Darwinulidae is needed to verify this hypothesis.

Taken together, the situation in genus *Lasaea* is the most complicated of all the studied AA groups from the viewpoint of present comparative study. *Lasaea* is highly understudied in this regard. Published literature does not offer enough information to investigate possible ecological differences among its AA lineages and sexual controls. In conclusion, available evidence is insufficient to identify any consistent differences in the biotic and abiotic heterogeneity of the environment of AA members of *Lasaea* and their sexual controls.

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