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COUVERTURE / *COVER*:

Some typical habitats of sub-Antarctic islands: wet coastal cliffs. Photo: Maurice Hullé.

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Terrestrial macro-arthropods of the sub-Antarctic islands of Possession (Crozet Archipelago) and Kerguelen: inventory of native and non-native species

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ABSTRACT

The sub-Antarctic islands of the Southern Ocean harbor biogeographically peculiar biotas which are under threat from climate change, biological invasions and their interactions. Understanding both the indigenous and changing non-indigenous components of these islands is essential for the conservation and management of their biotas. Based on several years of systematic sampling, we present an updated list of terrestrial, free-living macro-invertebrates (insects and spiders) present on the islands of Possession (Crozet Archipelago) and Kerguelen. Ninety-four species were recorded in total on both islands. Forty-one are strictly endemic to one of the two islands, 16 are endemic to the South Indian Ocean Province, and only three were recorded on other sub-Antarctic islands. Beetles and more particularly weevils are the most characteristic group of the fauna of these islands: they include 35 species of which 89% are native and 66% are endemic. One third of the species (30 of 94) are non-indigenous species now naturalized. We discuss these results in terms of biogeography, ecological disharmony and impact of biological invasions.

KEY WORDS
Introduced species,
endemic species,
Insecta,
Araneae,
species richness.

RÉSUMÉ

Les macro-arthropodes terrestres des îles subantarctiques de Possession (archipel Crozet) et des Kerguelen : inventaire des espèces natives et non-natives.

Les îles subantarctiques de l'océan Austral constituent des biotopes isolés et originaux, actuellement menacés par le changement climatique, les invasions biologiques et leurs interactions. Il est essentiel de comprendre les modifications de la faune autochtone et allochtone pour en assurer la conservation et la gestion. Sur la base de plusieurs années d'échantillonnage systématique, nous présentons une liste actualisée des macro-invertébrés terrestres libres (insectes et araignées) présents sur les îles Kerguelen et sur l'île de la Possession (archipel Crozet). Quarante-et-une espèces y ont été recensées au total. Quarante-et-une espèces sont strictement endémiques à l'une des deux îles, 16 sont endémiques à la province Antarctique de l'océan Indien, et seulement trois ont été recensées sur d'autres îles subantarctiques. Les coléoptères, et plus particulièrement les charançons, constituent le groupe le plus caractéristique de la faune de ces îles : ils comprennent 35 espèces, dont 89 % sont indigènes et 66 % sont endémiques. Un tiers des espèces présentes (30 sur 94) sont des espèces introduites aujourd'hui naturalisées. Nous discutons ces résultats en termes de biogéographie, de disharmonie écologique et d'impact des invasions biologiques.

MOTS CLÉS
Espèce introduite,
espèce endémique,
insectes,
aranéides,
richesse spécifique.

INTRODUCTION

The sub-Antarctic Islands of the South Indian Ocean (SIO) Province have well-developed biotas representing the only terrestrial life in a region dominated by ocean. These biotas are biogeographically and functionally unusual, given their complex relationships to the surrounding continents and characteristics such as outstanding high proportions of flightlessness among the insects (Roff 1990; Vernon *et al.* 1998; Leihy *et al.* 2018). Owing to these features and the significant numbers and global proportions of seabirds nesting on the islands, all of them enjoy significant conservation status (de Villiers *et al.* 2006), and most of them are now declared World Heritage Areas (Inscription of the French Austral Lands and Seas, France, on the World Heritage List, Decision n°43 COM 8B.6, https://whc.unesco.org/en/decisions/?id_decision=7362&). Nonetheless, the biotas of these islands face significant conservation challenges, among which the effects of climate change, biological invasions, and their interactions are most important (Frenot *et al.* 2005). Terrestrial invertebrates are considered especially vulnerable to such changes, including through the ongoing introduction of non-indigenous species (Lebouvier *et al.* 2011; Chown & Convey 2016; McClelland *et al.* 2018). The focus is thus on understanding these impacts and how best they might be mitigated and managed (Lebouvier *et al.* 2011; Preston *et al.* 2018). A critical aspect of doing so is to comprehensively understand the faunas, including their non-indigenous component, and how these are changing through time, either owing to impacts or to the establishment of new non-indigenous species (Heger *et al.* 2009; McGeoch *et al.* 2015).

Over the past decade, a range of systematic inventories or overviews of the biotas of the South Indian Ocean Province islands has been undertaken (reviewed in Chown & Convey [2016]). Some of them have been based on several years of systematic sampling at a given island or set of islands (e.g. Chown & Froneman 2008). Among these, however, the Kerguelen and Crozet islands have largely been under-studied. While new species discoveries and range extensions have been reported for some groups (e.g. Hullé *et al.* 2003b; Laporie 2011), comprehensive information was lacking. Such a situation is problematic given the biogeographical significance of these islands (Craig *et al.* 2003; Voisin *et al.* 2017), and the substantial threats facing their biotas from both climate change and biological invasions. Given this significance, the status of the islands as reserves, and their recent declaration as World Heritage Areas, there is an urgent need to provide a comprehensive updated inventory. Here we do so, for the macro-arthropods (spiders and insects), based on 12 years of systematic sampling, targeted searches for rare species, and recent developments in systematic knowledge of the biotas (Voisin *et al.* 2017; Broadley *et al.* 2018; Orlov *et al.* 2019).

Discovered at the end of the 18th century, the Crozet and Kerguelen islands have been visited many times since the 19th and early 20th centuries (Duhamel & Williams 2011), in a first step mainly by sea lions and elephant seals hunters, in a second step, and regularly, after the establishment of per-

manent scientific bases (Port-aux-Français at Kerguelen Is.; Alfred Faure at Possession Is.) in 1950 and 1960, respectively.

The indigenous species of the islands were initially recorded through successive scientific expeditions between 1840 and 1940, such as *Erebus* and *Terror* (1840), *Challenger* (1874), *Gazelle*, *Volage* and *Gauss* (1874), *Valdivia* (1898), *J. B. Charcot* (1908-1909) and *Bougainville* (1939), and then through scientific programs set up shortly after the permanent bases were built up. The first native species described were the weevil *Ectemnorhinus viridis* G. R. Waterhouse, 1853 and the snail *Notodiscus hookeri* (Reeve, 1854). Two thirds of the native species were then described before 1950 by scientists such as A. E. Eaton (Diptera), G. Enderlein (Coleoptera Linnaeus, 1758, Hemiptera Linnaeus, 1758, Diptera Linnaeus, 1758), V. V. Hickman (Araneae Clerck, 1757), R. Jeannel (Coleoptera), C. O. Waterhouse (Coleoptera). The remaining third of native species have been described since 1950. The first species introduced into the Kerguelen and Crozet Islands were mentioned following the Bougainville cruise in 1938-1939 with the entomologist R. Jeannel on board (Badonnel 1947; Jeannel 1940; Séguy 1940).

Species lists concerning particular islands or taxonomic groups and including native and alien species have also been published: entomofauna of Penguins Island (Crozet archipelago) (Dreux *et al.* 1988, 1993) and Apostles Islets (Crozet archipelago) (Vernon & Voisin 1990), aphids (Hullé *et al.* 2003a, b; Remaudière & Étienne 1988), spiders (Ledoux 1991), weevils (Chown 1992, 1994), and beetles (Voisin *et al.* 2017).

Our work builds on these previous studies, but also using annual systematic surveys and targeted searches for species known from the literature to have been previously recorded on the islands, but rarely found in recent times. The latter approach was adopted given evidence both from these islands (e.g. Renaud *et al.* 2013; Ouisse 2016) and elsewhere (McClelland *et al.* 2018) that environmental change impacts can have significant effects on the abundance and diversity of insect assemblages.

MATERIAL AND METHODS

STUDY AREA (Fig. 1)

Hereinafter, 'Kerguelen Is.' is used to refer to the main island called Grande Terre and all the peripheral islands except the Cloudy Islands and the Leygues Islands.

Both Kerguelen and Possession islands are in the middle of the South Indian Ocean. Kerguelen Is. is located at 49°21'S, 70°13'E and Possession Is. at 46°24'S, 51°46'E. They are respectively 3250 and 2800 km south of Reunion Is., 3800 and 2400 km south-east of South Africa and 1900 and 2100 km north of the Antarctic Continent. Kerguelen Is. and Heard Is. are located on the same continental shelf and are only 423 km apart. Crozet and the Prince Edward Islands are a second, more western sub-group and are 1063 km apart. Kerguelen Is. is 130 km long and 120 km wide. The total area is 7215 km² including 6675 km² for Grande Terre. Possession Is. is much smaller than Kerguelen Is., with only 150 km².

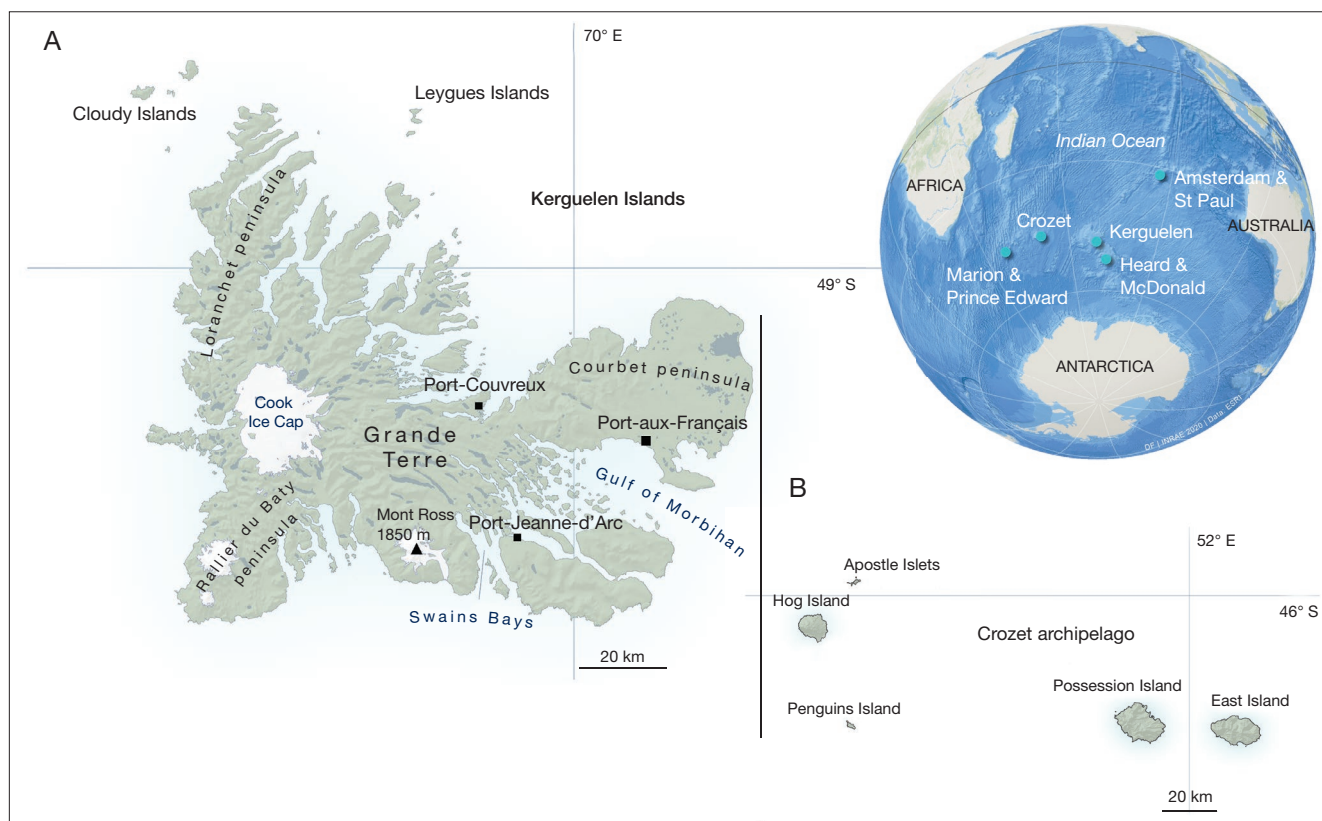


FIG. 1. — The South Indian Ocean sub-Antarctic islands, with details of Kerguelen Island (A) and Possession Island (B, in Crozet archipelago). Modified from D. Fourcy, Inrae, 2020.

The morphology of Kerguelen Is. is mainly related to its magmatic origin and glacial erosion. Its geological history is long. The most ancient parts emerged about 35 to 40 million years ago and the last magmatic events date back to about 30 000 years ago (Giret *et al.* 2003a). Mount Ross rises in the south to 1830 m. An ice cap rises to 1000 m and covers about 550 km² of the western and central region. The north and the west are mountainous and rise to 1260 m. The south-east constitutes a vast area of glacial erosion of low altitude and dotted with numerous lakes (Giret *et al.* 2003a). Possession Is. (elevation of 934 m) was formed between 8 million years ago and about 10 000 years ago (the last episodes of eruption) (Giret *et al.* 2003b).

Both islands have an oceanic cold climate, strongly influenced by the southern Indian Ocean. The annual mean air temperature at sea level (period 1973-2021) is 5.1° C at Kerguelen Is. and 5.4° C at Possession Is. Seasonal variations are low, between 2.3° C (coldest month) and 8° C (warmest month) at Kerguelen Is. and 2.9° C and 7.9° C at Possession Is. (data available on www.infoclimat.fr/globale/iles-kerguelen-port-aux-français/61998.html and www.infoclimat.fr/globale/ile-de-la-possession-alfred-faure/61997.html). Summer temperatures may temporarily reach 15° C. At Kerguelen Is. average temperatures increased by 1.9° C between 1964 and 1981 and then stabilized around 5.1° C. Correlatively the number of freezing days has decreased from 130 days per year in the 1960s to 100 days per year presently. At Possession Is.

the number of freezing days is less than 60 days per year. Air temperature decreases with *c.* 0.8° C per 100 m increase in altitude (Gremmen *et al.* 2007). This rapid decrease means that the development thermal thresholds of many insects are rapidly reached with elevation.

The average rainfall for Possession Is. is high with 2390 mm per year. For Kerguelen Is., there is a rainfall gradient from west to east. Port-aux-Français, located east of Kerguelen, receives only 700 mm a year. On Kerguelen Is., the rainfall oscillates between years of drought like 1965 with 350 mm and wetter years like 1987 with 1150 mm. Winds are predominantly from the north-west, west and south-west. Strong winds are frequent. The average wind speed is 35 km/h on Kerguelen Is. maximum speeds may exceed 200 km/h or 55 m/s (data from Météo France).

The main biotopes hosting terrestrial invertebrates are shown in Figure 2.

INVENTORY

All published records of species from the islands were initially considered based on a systematic search of the literature. All the species thus reported from the literature have been researched in the field using different approaches since the 2000s. First of all, we used the systematic field surveys on both islands as part of an ongoing research program of the French Polar Institute Paul Emile Victor (IPEV - Subanteco program: <http://www.institut-polaire.fr>). These surveys mainly consisted of

permanent sampling. Two pitfall traps and one yellow trap are regularly opened five days a month in three different sites in the vicinity of the research stations on each of the two islands. We compiled all of these sampling datasets and supplemented them with intensive field research in as many off-base sites as possible during five summer campaigns from 2007 to 2015. These complementary explorations were made by hand searching. In addition to these systematic surveys, dedicated searches for species listed as previously known from the islands, but not found during the systematic surveys, were also undertaken. For example, the weevils *Diskar tenuicornis* (Jeannel, 1940) and *Canonopsis sericea* C. O. Waterhouse, 1875 are known from a relatively small number of specimens in the Muséum national d'Histoire naturelle (MNHN) in Paris, but not seen during any of the systematic surveys. Targeted sampling for them, based on previous collection localities and discussions with experts were undertaken.

All material was identified based on 1) available keys such as Voisin *et al.* (2017) for Coleoptera or Séguy (1940) for Diptera and 2) a guide to the species that has been compiled based on these keys and on specialist taxonomic expertise (Hullé *et al.* 2018). The material collected on the field was then checked again on return to INRAE/Le Rheu. All identified specimens are kept at the UMR 6553 CNRS, ECOBIO of the University of Rennes 1 (Curator Romain Georges). Three reference collections have also been deposited, one at the UMR 6553 CNRS ECOBIO and the other two in each of the two scientific bases of the Kerguelen and Possession islands.

The species names used are mainly those of the INPN TAXREF (<https://inpn.mnhn.fr/programme/referentiel-taxonomique-taxref?lg=en>), an implementation of the national repository on fauna and flora of metropolitan France and overseas territories, and Encyclopedia of Life (<http://eol.org/>), unless very recent taxonomic revisions have not yet been incorporated into these two lists. In the case of weevil species described by either C. O. Waterhouse or G. R. Waterhouse, the first name initials have been added to distinguish these two authors.

Species were distinguished according to their native or introduced and naturalized nature (Falk-Petersen *et al.* 2006). Native species were separated into strict endemics (present on one of the two islands), endemics of the sub-Antarctic province of the Indian Ocean (present on at least two of Kerguelen, Crozet, Heard or Prince Edward Islands) or as sub-Antarctic species (if also present in the sub-Antarctic provinces of the Atlantic or Pacific Oceans) (Lewis Smith 1984).

RESULTS

In this section, we present the taxonomic results with comments clarifying these results, when necessary.

Ninety-four species of free-living macro-arthropods have been recorded to date on Kerguelen and Possession Islands (Tables 1, 2; Figs 3, 4). Thirty species are common to both islands.

Nearly one third of species (30 out of 94) are naturalized alien species. The native fauna is specific of the SOI

province: 41 species are strictly endemic to one of the two islands, 16 are endemic to the SIO province (present on at least two of the four groups of islands) and only three are also recorded on other sub-Antarctic islands, either of the South Atlantic Ocean or the New Zealand provinces. The number of introductions and the rate of endemism are different from one island to the other. On Possession Is., 29% of the species are alien compared to 56% on Kerguelen. Conversely, 49% of the species on Possession Is. are endemic compared to 12% on Kerguelen.

The orders including main native species are the Araneae, the Coleoptera and the Diptera. Together, they represent 79% and 77% of the native species on Possession Is. and Kerguelen Is., respectively. Other orders are poorly represented on both islands. Flies and aphids are the two main taxa of alien groups with 67% and 59% of the naturalized species on Possession Is. and Kerguelen Is., respectively.

ARACHNIDA CUVIER, 1812

Only two native spider species (from two families) are present on Kerguelen Is. compared to seven species (from four families) on Possession Is. On Possession Is. the family Desidae Pocock, 1895 comprises four out of five species present in the SIO province, among which *Myro jeanneli* Berland, 1947 and *M. pumilus* Ledoux, 1991 are endemic.

The naturalized alien species belong to three families, the Linyphiidae Blackwall, 1859 (three species), the Theridiidae Sundevall, 1833 (two species) and the Agelenidae Koch, 1837 (one species). Four of them (*Ostearius melanopygius* Pickard-Cambridge, 1879, *Tegenaria domestica* (Clerk, 1758), *Steatoda grossa* (Koch, 1838) and *S. triangulosa* (Walckenaer, 1802)) are confined to the buildings of the Alfred Faure scientific research base on Possession Is. and the Port-aux-Français research and administration facilities on Kerguelen Is. Only *Tenuiphantes tenuis* (Blackwall, 1852) can be abundant in the wild and is therefore considered invasive.

Opiliones and Pseudoscorpiones are uncommon and are each represented by only one endemic species on Possession Is.

COLEOPTERA

Coleoptera have the highest species richness with 31 native species and only four introduced species. This is particularly true on the Possession Is. where there is a single introduced species and 22 native species, 18 of which are endemic.

The family Curculionidae Latreille, 1802 is the best represented with 23 species including 17 strict endemics. Of the six species of weevils endemic to the SIO province, four are known from Kerguelen and Heard (*Bothrometopus brevis* (C. O. Waterhouse, 1875), *B. gracilipes* (C. O. Waterhouse, 1875), *Canonopsis sericea* and *Ectemnorhinus viridis*), and one on Possession and the Prince Edward Islands (*B. randi* Jeannel, 1953). Only *Palirhoeus eatoni* (C. O. Waterhouse, 1876) is present in the whole province. *Ectemnorhinus fuscus* Enderlein, 1903 has not been observed since its discovery in 1939 (Jeannel 1940) but it could have been confused with *E. viridis* (Voisin *et al.* 2017; Chapelin-Viscardi *et al.* 2010). This species is therefore counted but not yet validated.



FIG. 2. — Some typical habitats of sub-Antarctic islands: **A**, wide open valley; **B**, wet coastal cliffs; **C**, slopes covered with *Acaena magellanica*; **D**, fell field; **E**, native vegetation; **F**, introduced vegetation; **G**, coastal slopes and foreshore; **H**, marine animal colonies. Photos: Maurice Hullé.



FIG. 3. — Some indigenous arthropod species : Arachnida : **A**, *Hahnia crozetensis* Hickman, 1939; **B**, *Myro paucispinosus* Berland, 1947; Coleoptera : **C**, *Ectemnorhinus viridis* G. R. Waterhouse, 1853; **D**, *Palirhoeus eatoni* (C. O. Waterhouse, 1876); **E**, *Amblystogenium pacificum* (Putzeys, 1869); **F**, *Meropathus chuni* Enderlein, 1901; Diptera : **G**, *Calycopteryx moseleyi* Eaton, 1875; **H**, *Anatalanta aptera* Eaton, 1875. Photos: Bernard Chaubet.

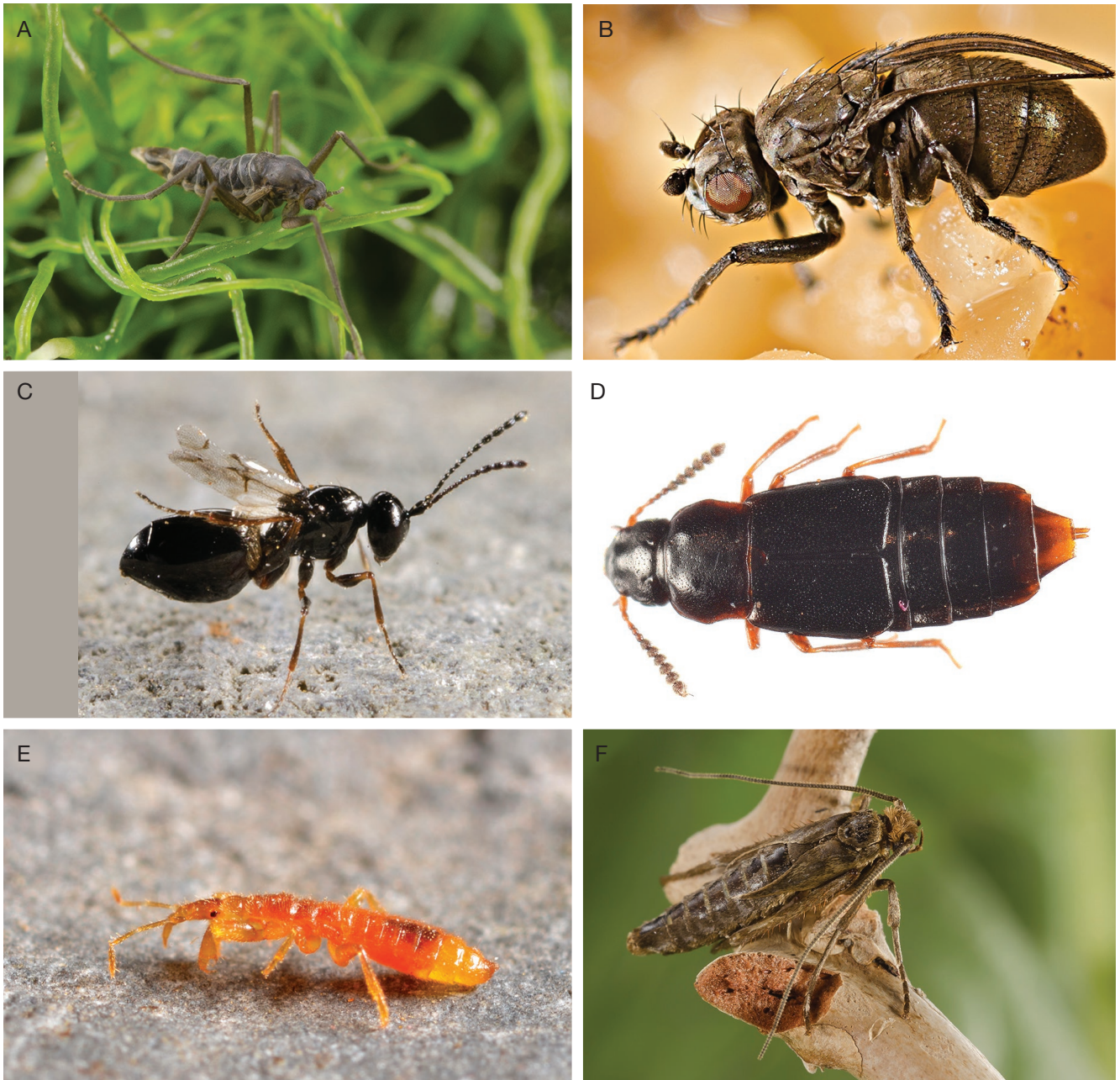


FIG. 4. — Some indigeneous arthropod species : Diptera: **A**, *Telmatogeton amphibius* (Eaton, 1875); **B**, *Amalopteryx maritima* Eaton, 1875; Hymenoptera: **C**, *Kleidotoma icarus* (Quinlan, 1964); Coleoptera: **D**, *Antarctotachinus crozetensis* Enderlein, 1909; Hemiptera: **E**, *Phthirocoris antarcticus* Enderlein, 1904; Lepidoptera: **F**, *Pringleophaga kerguelensis* Enderlein, 1905. Photos: Bernard Chaubet.

Among the family Staphylinidae Latreille, 1802, the indigenous species, *Leptusa atriceps* (C. O. Waterhouse, 1875), is the one with the broadest distribution being also present on the sub-Antarctic islands of the southern Atlantic Ocean (Falkland Islands and South Georgia) (Gressitt 1970; Craford *et al.* 1986; Orlov *et al.* 2019).

The family Trechidae Bonelli, 1810 is worth studying because it comprises three endemic species on Possession Is. and a single introduced species, *Merizodus soledadinus* (Guérin-Ménéville, 1830) on Kerguelen. The expansion of this predatory species has currently a dramatic effect on the

native fauna and in particular on the Diptera (Chevrier *et al.* 1997; Lebouvier *et al.* 2011; Lebouvier *et al.* 2020).

DIPTERA

Diptera is the second-most speciose order with 27 species on both islands. It is also the most diverse with 15 families, eight of which include native species. Diptera also include 11 alien species. Three taxa were not yet identified to species, but currently under study: one Carnidae Newman, 1834 and two Chironomidae Newman, 1834 (*Smittia* sp. and *Bryophaenocladus* sp.).

TABLE 1. — Free-living macro-arthropod species recorded on Kerguelen and Possession Islands. Abbreviations: conservation status: **End**, endemic; **Int**, introduced and established; **SIO**, South Indian Ocean Province; **Sub-Ant**, sub-Antarctic. Distribution: **F**, Falkland; **H**, Heard; **K**, Kerguelen Is.; **Mc**, Macquarie; **PE**, Prince Edward Islands; **Po**, Possession Is.; **SG**, South Georgia. Symbols: *, presence; –, absence.

Species	Possession Is.	Kerguelen Is.	Conservation status	Distribution	Species	Possession Is.	Kerguelen Is.	Conservation status	Distribution
Arachnida Araneae					<i>Bothrometopus sulcatus</i> Jeannel, 1953	–	*	End	K
Agelenidae					<i>Canonopsis sericea</i> C.O. Waterhouse, 1875	–	*	SIO	H K
<i>Tegenaria domestica</i> (Clerck, 1758)	–	*	Int	–	<i>Christensenia antarctica</i> Brinck, 1945	*	–	End	Po
Anapidae					<i>Diskar tenuicornis</i> (Jeannel, 1940)	–	*	End	K
<i>Crozetus minutus</i> Hickman, 1939	*	–	End	Po	<i>Ectemnorhinus bougainvillei</i> Jeannel, 1940	*	–	End	Po
Desidae					<i>Ectemnorhinus drygalskii</i> Enderlein, 1909	–	*	End	K
<i>Myro jeanneli</i> Berland, 1947	*	–	End	Po	<i>Ectemnorhinus fuscus</i> Enderlein, 1903	–	*	End	K
<i>Myro kerguelenensis crozetensis</i> Enderlein, 1909	*	–	SIO	Po PE	<i>Ectemnorhinus geniculatus</i> Jeannel, 1940	*	–	End	Po
<i>Myro kerguelenensis kerguelenensis</i> Pickard-Cambridge, 1876	–	*	Sub-Ant	H K Mc	<i>Ectemnorhinus richtersi</i> Enderlein, 1904	*	–	End	Po
<i>Myro paucispinosus</i> Berland, 1947	*	–	SIO	Po PE	<i>Ectemnorhinus viridis</i> G.R. Waterhouse, 1853	–	*	SIO	H K
<i>Myro pumilus</i> Ledoux, 1991	*	–	End	Po	<i>Neocanonopsis dreuxi</i> (Hoffmann, 1966)	*	–	End	Po
Hahniidae					<i>Palirhoeus eatoni</i> (C.O. Waterhouse, 1876)	*	*	SIO	Po H K PE
<i>Hahnia crozetensis</i> Hickman, 1939	*	–	End	Po	<i>Xanium possessionense</i> Hoffmann, 1966	*	–	End	Po
Linyphiidae					<i>Xanium vanhoeffenianum</i> Enderlein, 1904	*	–	End	Po
<i>Lepthyphantes leprosus</i> (Ohlert, 1865)	–	*	Int	–	Hydraenidae				
<i>Neomaso antarcticus</i> (Hickman, 1939)	–	*	End	K	<i>Meropathus chuni</i> Enderlein, 1901	–	*	End	K
<i>Ostearius melanopygius</i> Pickard-Cambridge, 1879	*	–	Int	–	<i>Meropathus randi</i> Jeannel, 1953	*	–	SIO	Po PE
<i>Ringina antarctica</i> (Hickman, 1939)	*	–	End	Po	Latridiidae				
<i>Tenuiphantes tenuis</i> (Blackwall, 1852)	–	*	Int	–	<i>Cartodere nodifer</i> (Westwood, 1839)	*	*	Int	–
Pholcidae					<i>Latridius minutus</i> (Linnaeus, 1767)	–	*	Int	–
<i>Pholcus phalangioides</i> (Fuessly, 1775)	*	–	Int	–	Ptinidae				
Theridiidae					<i>Ptinus tectus</i> Boieldieu, 1856	–	*	Int	–
<i>Steatoda grossa</i> (Koch, 1838)	*	*	Int	–	Staphylinidae				
<i>Steatoda triangulosa</i> (Walckenaer, 1802)	*	*	Int	–	<i>Antarctotachinus crozetensis</i> Enderlein, 1909	*	–	End	Po
Arachnida Opiliones					<i>Leptusa atriceps</i> (C.O. Waterhouse, 1875)	*	*	Sub-Ant	SIO, F, SG
Trianenychidae					<i>Pseudeupectus antarcticus</i> Enderlein, 1909	*	–	End	Po
<i>Promecostethus unifalculatus</i> Enderlein, 1909	*	–	End	Po	Trechidae				
Arachnida Pseudoscorpiones					<i>Amblystogenium minimum</i> Luff, 1972	*	–	End	Po
Chthoniidae					<i>Amblystogenium pacificum</i> (Putzeys, 1869)	*	–	End	Po
<i>Austrochthonius insularis</i> Vitali de Castri, 1968	*	–	End	Po	<i>Merizodus soledadinus</i> (Guérin-Méneville, 1830)	–	*	Int	–
Coleoptera					<i>Temnostega antarctica</i> Enderlein, 1905	*	–	End	Po
Curculionidae					Diptera				
<i>Bothrometopus angusticollis</i> (C.O. Waterhouse, 1875)	–	*	End	K	Anthomyiidae				
<i>Bothrometopus brevis</i> (C.O. Waterhouse, 1875)	–	*	SIO	H K	<i>Fucellia tergina</i> (Zetterstedt, 1845)	*	*	Int	–
<i>Bothrometopus comes</i> Chown & Kuschel, 1994	*	–	End	Po	Calliphoridae				
<i>Bothrometopus crozetensis</i> (Enderlein, 1904)	*	–	End	Po	<i>Calliphora vicina</i> Robineau-Desvoidy, 1830	–	*	Int	–
<i>Bothrometopus daviesi</i> Chown & Kuschel, 1994	*	–	End	Po	Canacidae				
<i>Bothrometopus desolationis</i> (Jeannel, 1940)	*	–	End	Po	<i>Apetaenus enderleini</i> (Enderlein, 1909)	*	*	SIO	Po K PE
<i>Bothrometopus fasciatus</i> Jeannel, 1940	*	–	End	Po	<i>Apetaenus litoralis</i> Eaton, 1875	*	*	SIO	Po K PE
<i>Bothrometopus gracilipes</i> (C.O. Waterhouse, 1875)	–	*	SIO	H K					
<i>Bothrometopus gravis</i> Chown & Kuschel, 1994	*	–	End	Po					
<i>Bothrometopus randi</i> Jeannel, 1953	*	–	SIO	Po PE					

TABLE 1 — Continuation.

Species	Possession Is.	Kerguelen Is.	Conservation status	Distribution	Species	Possession Is.	Kerguelen Is.	Conservation status	Distribution
Carnidae					Trichoceridae				
Species 1	*	*	Int	–	<i>Trichocera maculipennis</i> Meigen, 1818	–	*	Int	–
Chironomidae					Hemiptera				
<i>Belgica albipes</i> (Séguy, 1965)	*	–	End	Po	Aphididae				
<i>Bryophaenocladus</i> sp Thienemann, 1934	*	*	Int	–	<i>Aulacorthum solani</i> (Kaltenbach, 1843)	*	*	Int	–
<i>Limnophyes minimus</i> (Meigen, 1818)	*	*	Int	–	<i>Macrosiphum euphorbiae</i> (Thomas, 1878)	*	*	Int	–
<i>Microzetia mirabilis</i> Séguy, 1965	*	–	End	Po	<i>Myzus ascalonicus</i> Doncaster, 1946	*	*	Int	–
<i>Parochlus crozetensis</i> Serra-Tosio, 1986	*	–	End	Po	<i>Myzus ornatus</i> Laing, 1932	*	*	Int	–
<i>Smittia</i> sp Holmgren, 1869	–	*	Unknown	–	<i>Myzus persicae</i> (Sulzer, 1776)	–	*	Int	–
<i>Telmatogeton amphibius</i> (Eaton, 1875)	*	*	SIO	Po K PE	<i>Rhopalosiphum padi</i> (Linnaeus, 1758)	*	*	Int	–
Ephydriidae					Enicocephalidae				
<i>Amalopteryx maritima</i> Eaton, 1875	*	*	Sub-Ant	Po K H Mc	<i>Phthirocoris antarcticus</i> Enderlein, 1904	*	–	End	Po
Helcomyzidae	–	–	–	–	Hymenoptera				
<i>Paractora dreuxi</i> Séguy, 1965	*	–	SIO	Po PE	Figitidae				
Micropezidae	–	–	–	–	<i>Kleidotoma icarus</i> (Quinlan, 1964)	*	*	SIO	Po K PE
<i>Calycopteryx moseleyi</i> Eaton, 1875	–	*	SIO	H K	Lepidoptera				
Keroplastidae					Plutellidae				
<i>Macrocera crozetensis</i> Colless, 1970	*	–	End	Po	<i>Embryonopsis halticella</i> Eaton, 1875	*	*	SIO	H K PE
Psychodidae					Tineidae				
<i>Psychoda parthenogenetica</i> Tonnoir, 1940	*	*	Int	–	<i>Pringleophaga crozetensis</i> Enderlein, 1905	*	–	End	Po
Scatopsidae	–	–	–	–	<i>Pringleophaga kerguelensis</i> Enderlein, 1905	*	*	SIO	Po K PE
<i>Scatopse notata</i> (Linnaeus, 1758)	*	*	Int	–	Psocoptera				
Sciaridae					Elipsocidae				
<i>Lycoriella sativae</i> (Johannsen, 1912)	*	*	Int	–	<i>Antarctopsocus daviesi</i> Badonnel, 1970	*	–	End	Po
<i>Lycoriella ingenua</i> (Dufour, 1839)	*	*	Int	–	Trogiidae				
Simuliidae					<i>Lepinotus patruelis</i> Pearman, 1931	–	*	Int	–
<i>Crozetia crozetensis</i> (Womersley, 1937)	*	–	End	Po	Psoquillidae				
<i>Crozetia seguyi</i> Beaucournu-Saguez & Vernon, 1990	*	–	End	Po	<i>Rhyopsocus eclipticus</i> Hagen, 1876	*	*	Int	–
Sphaeroceridae					Thysanoptera				
<i>Anatalanta aptera</i> Eaton, 1875	*	*	SIO	Po H K	Thripidae				
<i>Anatalanta crozetensis</i> Enderlein, 1908	*	–	End	Po	<i>Apterothrips apteris</i> (Daniel, 1904)	*	*	Int	–
<i>Leptocera curvinervis</i> (Stenhammar, 1855)	*	*	Int	–					
<i>Siphlopteryx antarctica</i> Enderlein, 1909	*	–	End	Po					

Kerguelen Is. hosts more introduced species than native ones. We know that *Fucellia tergina* (Zetterstedt, 1845), *Limnophyes minimus* (Meigen, 1818) and Sciaridae Billberg, 1820 species were introduced before the end of the first half of the 20th century because they were already observed by Jeannel during the Bougainville expedition to Kerguelen in 1938-1939 (Séguy 1940). Séguy described three new species of sciarids from Jeannel's collection (Séguy 1940), but a recent study has reclassified them into two species, *Lycoriella sativae* (Johannsen, 1912) and *Lycoriella ingenua* (Dufour, 1839), both likely introduced (Broadley *et al.* 2018). *Fucellia tergina* first observed by Jeannel was neither observed in

1965 (Dreux 1966) nor in 1968 (Davies 1973). It was then regularly observed by the scientists of the IPEV-Subanteco program and is now one of the most widespread insect species.

Calliphora vicina Robineau-Desvoidy, 1830 was first observed on Kerguelen Is. in 1978. Its expansion was then favored by rising temperatures in the 1980s (Frenot *et al.* 2005; Lebouvier *et al.* 2011). More recently, other species were introduced and are now naturalized: *Leptocera curvinervis* (Stenhammar, 1855) since 2003 on Kerguelen, *Scatopse notata* (Linnaeus, 1758) since 2004 on Kerguelen and 2017 on Possession Is., Carnidae sp. since 2007 on Kerguelen Is. and 2013 on Possession Is.

TABLE 2. — Status of species according to their level of endemism. Abbreviation: SIO, South Indian Ocean.

Order	Naturalized	Endemic	SIO	Sub-antarctic	Unknown	Total
Possession Is.	4	5	2	–	–	11
Opiliones	–	1	–	–	–	1
Pseudoscorpiones	–	1	–	–	–	1
Coleoptera	1	18	3	1	–	23
Diptera	9	8	5	1	–	23
Hemiptera	5	1	–	–	–	6
Hymenoptera	–	–	1	–	–	1
Lepidoptera	–	1	2	–	–	3
Psocoptera	1	–	1	–	–	2
Thysanoptera	1	–	–	–	–	1
Total	21	35	14	2	–	72
Kerguelen Is.						
Araneae	5	1	–	1	–	7
Coleoptera	4	5	5	1	–	15
Diptera	11	–	5	1	1	18
Hemiptera	6	–	–	–	–	6
Hymenoptera	–	–	1	–	–	1
Lepidoptera	–	–	2	–	–	2
Psocoptera	1	–	1	–	–	2
Thysanoptera	1	–	–	–	–	1
Total	28	6	14	3	1	52

HEMIPTERA

With the exception of the small edaphic bug, *Phthirocoris antarcticus* Enderlein, 1904, endemic to Crozet, this order is represented only by introduced species belonging to the family Aphididae Latreille, 1802. Six aphid species were introduced and have established (Hullé *et al.* 2003b). *Myzus ascalonicus* Doncaster, 1946 and *Rhopalosiphum padi* (Linnaeus, 1758) are the two most common species in the wild. *Myzus ascalonicus*, first observed in the 1960s (J.-F. Voisin, pers. comm.) has become the most invasive insect species on Kerguelen, being present in all locations where it was sought. *Macrosiphum euphorbiae* (Thomas, 1878) was first introduced on Possession Is. (Hullé *et al.* 2003b). Observed for the first time on Kerguelen in 2012, it is currently expanding its range on Kerguelen. Initially confined to the immediate vicinity of the base, it is now regularly observed at a distance of 10 km to the south-east since 2014 or 20 km to the west since 2016. In contrast, *Myzus persicae* (Sulzer, 1776) appears to be in significant decline. Observed for the first time in 2000 in a greenhouse at Port-aux-Français and then outside, it has not been observed since 2010.

Other species are regularly seen during passages of the supply boat. Most certainly brought with fresh food, these species have so far never been able to establish themselves. Thus *Nasonovia ribisnigri* (Mosley, 1841) on lettuce and *Brachycaudus helichrysi* (Kaltenbach, 1843) on various vegetables are often detected on bases just after the ship stopovers.

HYMENOPTERA LINNAEUS, 1758

The order Hymenoptera includes only one species, *Kleidotoma icarus* (Quinlan, 1964) which is native and present in SIO province. This is a flightless parasitoid of sub-Antarctic flies.

LEPIDOPTERA LINNAEUS, 1758

Only three native Lepidoptera species have been recorded on both islands. This order does not present any naturalized alien species. Some alien species are however regularly observed especially on Possession Is., but remain transient without reproducing. The Nymphalidae Rafinesque, 1815 *Vanessa cardui* (Linnaeus, 1758) is thus frequently observed on Possession Is. during transoceanic flights as well as on Marion Is. (Crafford *et al.* 1986; Hänel 1999). In the same way, observations of a Noctuidae Latreille, 1809 (*Agrotis* sp.) took place recently. This species does not seem to be *Agrotis ipsilon* (Hufnagel, 1766) which was already recorded on Possession Is. in 1972 (Barbut & Voisin 2014), Marion (Crafford *et al.* 1986), Macquarie (Greenslade *et al.* 1999) and South Georgia in 2000 (Convey 2005). In 2018, a living specimen of the Pyralidae Latreille, 1809 *Plodia interpunctella* (Hübner, 1813) was recorded in one of the buildings of the Alfred Faure base. It was probably introduced with dried goods.

PSOCOPTERA SHIPLEY, 1904

The order Psocoptera was known by four species previously reported from the islands but these descriptions are confused and the status of these species needs to be revised. At present, only two species are retained. *Antarctopsocus daviesi* Badonnel, 1970 was considered endemic to Crozet, but it has been recently reported also from Kerguelen. The second species, *Leptinotus patruelis* Pearman, 1931 was introduced to both islands.

THYSANOPTERA HALIDAY, 1836

Only one species of Thysanoptera, *Apterothrips apteris* (Daniel, 1904), occurs on both Kerguelen and Possession Islands. This introduced species was first observed on Crozet in 1968 (Davies 1973) and has also been reported from the Prince Edward Islands (Crafford *et al.* 1986; Barendse & Chown 2001).

REMARK

Despite the increase in sub-Antarctic invertebrate knowledge, complementary taxonomic studies are still needed for a few groups. These include: 1) identifications that need to be completed; 2) taxonomic problems that need to be resolved; and 3) possible intraspecific variability (at the scale of an island or between the two islands) that needs to be investigated (Table 3).

DISCUSSION

AN ENIGMATIC NATIVE FAUNA

The biogeographical origin of the fauna of the Kerguelen and Possession Islands is far from being elucidated. Jeannel (1965) pointed out that a significant part of the native fauna of the sub-Antarctic islands (and mainly that of Possession Island) has similarities with species from southern and eastern Africa. These species are the Coleoptera *Amblystogenium pacificum* Luff, 1972, *Antarctotachinus crozetensis* Enderlein, 1909, *Pseudoplectus antarcticus* Enderlein, 1909, the Diptera

TABLE 3. — Complementary taxonomic studies in progress.

Order/Family	Taxa	Study	Collaboration
Arachnida Triaenonychidae	<i>Promecostethus unifalcalatus</i> Enderlein, 1909	Intraspecific variability	Dr W. Porto, Museum Argentino de Ciencias Naturales, Buenos Aires, Argentina
Coleoptera Curculionidae		Taxonomic revision	Dr S. L. Chown, H.P. Baird, Monash University, Melbourne, Australia Dr R. Oberprieler, CSIRO, Canberra, Australia
Diptera Carnidae	species 1	Identification	Dr R. Meier, National University of Singapore, Singapore
Chironomidae	<i>Briophaenocladus</i> sp. <i>Smittia</i> sp.	Identification	T. Ekrem, NTNU University Museum, Trondheim, Norway

Siphlopteryx antarctica Enderlein, 1909, the Hemiptera *Phtirocoris antarcticus*, and the spiders *Hahnia crozetensis* Hickman, 1939 and *Crozetulus minutus* Hickman, 1939. Jeannel's hypothesis was based on the putative existence of a continental bridge between Africa, Madagascar and the sub-Antarctic islands, which would now have disappeared. However, this hypothesis is today highly controversial: the recent geological history of the Crozet Islands made it possible to convincingly refute this hypothesis (see e.g. Meyzen *et al.* 2016). To explain these similarities, other hypotheses must therefore be considered. They all depend on air or sea transport from Africa to Crozet: active flight, airborne drift, hitching a ride on other animals, or rafting on floating objects. But the geographical position, the distance to be covered and the time required to cover it (which presupposes a significant capacity for survival) make such assumptions unlikely. This debate therefore remains open.

The extreme geographic isolation of these oceanic islands does not currently explain why the number of the native free macroarthropods is higher on Possession Is. than on Kerguelen Is., which is almost 50 times larger. Similarly, despite its much smaller size and much more recent geological age, Possession Is. hosts almost six times more endemic species than Kerguelen Is. (Table 2). This noteworthy difference has been discussed by Craig (2003) and Craig *et al.* (2003), and is not yet completely understood.

TAXONOMIC AND FUNCTIONAL DISHARMONY OF NATIVE FAUNA

Sixty years ago, Gressitt & Weber (1959) already emphasized the disharmonic nature of the sub-Antarctic entomofauna, a remarkable feature Gressitt latter considered in greater detail (Gressitt 1970). Two holometabolous insect orders, Coleoptera and Diptera account for 71% and 75% of the native macroarthropod species on Possession Is. and Kerguelen Is., respectively. Orders usually well represented in temperate fauna such as Lepidoptera and Hymenoptera have very few species here. Functional disharmony is often associated to taxonomic disharmony: when only insects are considered, the dominance of decomposers, the comparatively low number of phytophagous species, and the deficiency of predatory species in sub-Antarctic terrestrial food-webs have often been noted

(e.g. Vernon *et al.* 1998). This statement must however be modulated with the progress in the taxonomic knowledge of sub-Antarctic weevils as phytophagous species (Voisin *et al.* 2017) and also when spiders as predators are taken into account in this kind of analysis.

ANTHROPOGENIC CHANGES IN NATIVE FAUNA

Since the discovery by humans of these two archipelagos, the arrival of non-native species from the continents or the transport of native species between the different archipelagos of the Indian Ocean or between the islands of the same archipelago have been made possible because of a significant number of human visitors since the 19th century (Basberg & Headland 2008; Duhamel & Williams 2011). The introduction of non-native species has then been accelerated since the establishment of permanent bases in the middle of the 20th century. Twenty years ago, 14% and 33% of naturalized aliens were observed in Possession Is. and Kerguelen Is., respectively (Chown *et al.* 1998), when in the current work these percentages reach 26% (Possession Is.) and 53% (Kerguelen Is.). Increasing temperatures very likely play a key role for the establishment of non-native species (Lebouvier *et al.* 2011). The establishment of species belonging to orders already present on the islands such as spiders, beetles or flies has generated competitive phenomena. This is the case, for example, of the ground beetle *Merizodus soledadinus* which has become the main predator of native species such as *Anatalanta aptera* or the blowfly *Calliphora vicina* which lays eggs in the same corpses as *A. aptera* but with a greater efficiency (Chapuis *et al.* 1995; Lebouvier *et al.* 2020). The functioning of food webs has also been disrupted by the introduction of non-existent functional groups such as sap-feeding insects. Five aphid species have been introduced since the 1960s, including *Myzus ascalonicus*, which is extremely invasive and feeds preferentially on native plants (Hullé 2012) and *Rhopalosiphum padi*, which has transmitted phytopathogenic viruses to the native plant *Poa cookii* Hook.f., 1879 (Svanella-Dumas *et al.* 2013). It is now important to adhere to and even amplify the control measures put in place in 2006 with the creation of a nature reserve in order to limit as much as possible the arrival and, above all, the installation and expansion of new species.

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