



# The first study on Chinese marine ostracods revisited: historical ecology of Hong Kong ostracods

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**Abstract.** The pioneering study of Chinese marine ostracods was done by George Stewardson Brady using specimens from Hong Kong in the 19th century. Since then, Robin C. Whatley and Quanhong Zhao restudied Brady's Hong Kong materials by using a scanning electron microscope (SEM) in the 1980s. Whatley and Zhao's studies substantially reduced the taxonomic uncertainty of Brady's Hong Kong species. These studies provide important information on the historical ecology of the less urban 19th-century Hong Kong, especially in comparison with a recent comprehensive survey on Hong Kong ostracods. Here, we (1) show a full list of Hong Kong ostracods studied by Brady with up-to-date taxonomy and then (2) compare Hong Kong ostracod species in Brady's 19th-century study and in a comprehensive 21st-century survey. Our comparison is qualitative and has limitations with uncertainties related to Brady's 19th-century study. Our results nonetheless indicate that four ostracod species known to be sensitive to pollution, eutrophication, or deoxygenation were reported in Brady's study, with only one tolerant species being reported there, whereas tolerant species tend to be much more abundant compared to sensitive species in Hong Kong in the 21st century. Brady also reported > 10 species which are now rare in Hong Kong. These species might have been more abundant in the 19th century because of pre-industrial, near-pristine environments. In addition, many of these rare species are known as tropical species, and, at the same time, several temperate species now abundant in Hong Kong were not reported by Brady. Hong Kong's sea surface temperature is known to have been ~ 1–2 °C higher ~ 100 years ago than in the present. This recent cooling may have diminished the tropical species and aided the temperate species in subtropical Hong Kong. Our results suggest that the marine environment in 19th-century Hong Kong was much healthier, so the abundance of tolerant species was lower, giving Brady a lower chance to encounter them. He also had a better chance of finding tropical species in subtropical Hong Kong because of warmer sea temperatures at that time. These results highlight the importance of historical ecology by revisiting zoological studies by natural historians in the 19th and early 20th centuries. They documented a “natural baseline” ecosystem before the substantial human presence with industrialization.

## 1 Introduction

Marine ostracods in China were first studied by British zoologist George Stewardson Brady using Hong Kong specimens in the 19th century (Brady, 1869). Brady described new species and reported species that he identified as known species from elsewhere. Robin C. Whatley and Quanhong Zhao restudied Brady's ostracods deposited in the Hancock Museum (now in the Discovery Museum; David Horne, personal communication, 2023), Newcastle-upon-Tyne, UK, and in the Centre d'Études et de Recherches Scientifiques, Biarritz, France, especially species described by Brady as new there (Whatley and Zhao, 1988a; Zhao and Whatley, 1988). Their work substantially reduced taxonomic uncertainty by using a scanning electron microscope (SEM) and thus provided a much better objective observation of their morphology than hand drawings in the 19th century.

After British colonization in the 1840s, Hong Kong developed as a British Crown colony by the late 1800s and experienced industrialization (such as the start of a tramway in the 1890s) (Kestell and Meinheit, 1997). Hong Kong's population increased from ~7000 in 1841, when Hong Kong was settled by scattered fishing and rice farming villages, to 0.8 million in 1931, and it increased to > 1.6 million in 1941 as a result of Chinese immigrants in Hong Kong due to the Sino-Japanese War (Fig. 1) (Kestell and Meinheit, 1997; Meacham, 1999; Evans, 2017). During the time of the Japanese occupation, Hong Kong's population decreased from ~1.6 million to 0.6 million. After the war, the population recovered to ~2.2 million by 1950. A rapid population increase and industrialization, shifting Hong Kong to a manufacturing economy, occurred from the 1950s (Kestell and Meinheit, 1997; Dudgeon and Corlett, 2004). Since the late 1990s and 2000s, Hong Kong has become a financial and service center, with the manufacturing industry moving to mainland China, e.g., Shenzhen. Rice cultivation was gradually abandoned in the late 20th century (Yang et al., 2018). In the 1970–1980s, scientists gradually recognized substantial marine problems, such as pollution, eutrophication, overfishing, land reclamation, and invasive species (Trott and Fung, 1973; Morton, 1987, 1988, 1989). New pollutants continuously emerged in the late 20th and 21st centuries (Lai et al., 2016; Ruan et al., 2022). Hong Kong's marine biologists extensively documented the process of degradation of marine ecosystems, such as changes in marine communities and the disappearance of corals, and rapidly increased knowledge of these issues, especially during the 1980s (Morton, 1976, 1989, 1994), along with the issue of overfishing since the mid-to-late 20th century (Cheung and Sadovy, 2004; Tao et al., 2018). However, the deepest roots of the ecological impacts of these problems or natural baselines are obscure, and this is known as shifting baseline syndrome (Pauly, 1995), because marine biological studies in Hong Kong essentially started in the 1970s and data on the situation prior to the 1970s are rare. The reclamation of coastal

areas is known to have started from the 1840s (Ng and Cook, 1997; Lai et al., 2016). Sediment core studies indicate that Hong Kong's marine pollution started in the 1940s or 1950s (Fung and Lo, 1997; Tang et al., 2008; Wei et al., 2008). Some human-induced environmental deterioration, such as eutrophication and overexploitation, could extend back to historic, pre-industrial, and even ancient Chinese dynasty periods related, for example, to deforestation, overfishing, and lime kiln use (Dudgeon and Corlett, 2004). However, ecological impacts from such early human activities before the 1970s have rarely been documented (Morton, 1988). In addition, climatic changes have very likely affected Hong Kong's marine ecosystems. An essential way of knowing ancient ecosystems beyond the period of contemporary scientific observation is through historical ecology by using historical documentation, photography, illustrations (Lotze and McClenachan, 2014), and natural history collections (Fox et al., 2020; Rillo et al., 2019).

As summarized above and also obviously illustrated in Fig. 1, Hong Kong is substantially different between the 19th century and the 21st century in its development and thus most likely in its ecosystems and in the human-induced impacts on them. However, we do not know the pre-industrial, 19th-century marine ecosystems of Hong Kong, which is situated on the northern tip of the highly biodiverse Coral Triangle biodiversity hotspot with high conservation importance (Ng et al., 2017). Hong Kong ostracods reported by Brady (1869) are first-class material for historical ecology and give us a unique opportunity to compare ostracod faunas between the 19th and 21st centuries. Here, we compare Hong Kong ostracod faunas in the 19th and 21st centuries by using Brady's study (Brady, 1869) and a recent comprehensive survey by our research group (Hong et al., 2019, 2022).

## 2 Methods

We updated the list of marine benthic ostracod species reported by Brady (1869) to contemporary taxonomy (i.e., species names) based on Zhao and Whatley's restudy of Brady's original materials (Whatley and Zhao, 1988a; Zhao and Whatley, 1988) and other ostracod taxonomy papers in Hong Kong (Wang and Zhang, 1987; Cao, 1998; Wang et al., 2019) and beyond (Whatley and Zhao, 1987, 1988b; Hou and Gou, 2007). However, because of (1) uncertainties in labeling of some of the original slides (Whatley and Zhao, 1988a), (2) a lack of illustrations in Brady (1869) or of SEM images in Zhao and Whatley's restudies (Whatley and Zhao, 1988a; Zhao and Whatley, 1988) (note that Brady mainly illustrated new species and that most known species are just listed without illustrations. Zhao and Whatley also focused mostly on Brady's new species), and (3) broader species concepts at that time (and resulting misidentifications), uncertainties remain for some species. In such cases, we tried to estimate contemporary and correct species names based on

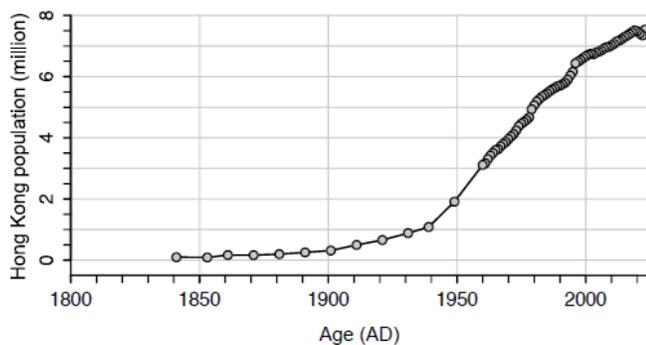
(a) Hong Kong Island 2024



(b) Hong Kong Island 1862



(c)



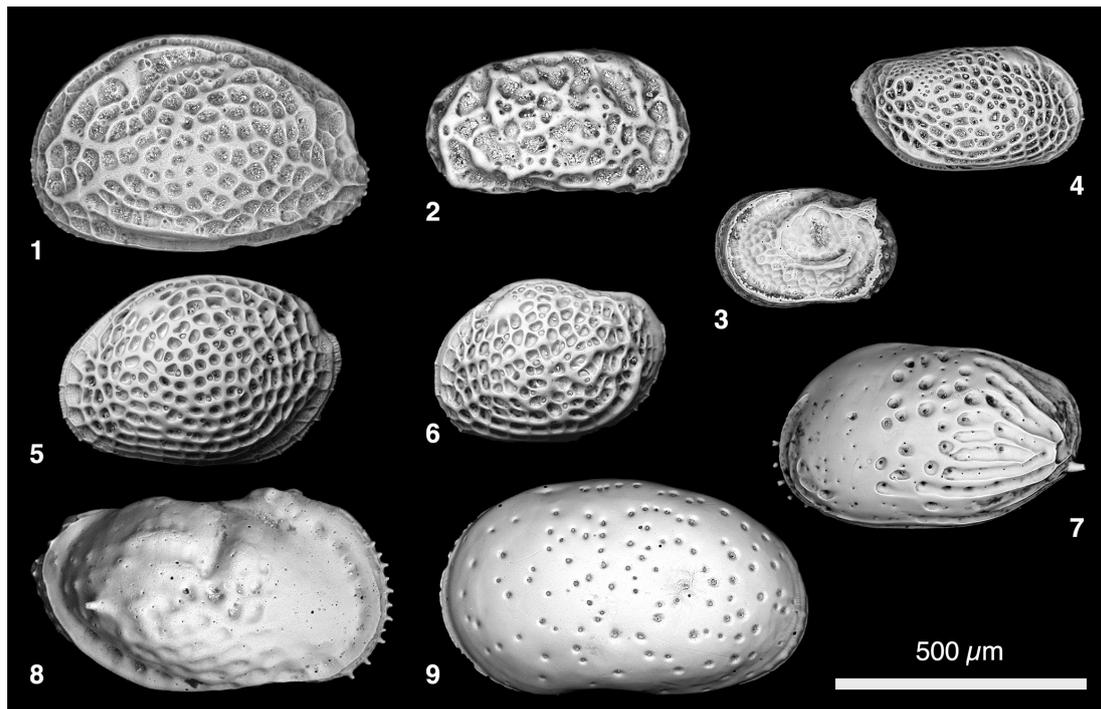
**Figure 1.** Comparing 19th-century and 21st-century Hong Kong. (a) A picture of 21st-century Hong Kong (Hong Kong Island and Victoria Harbour in 2024; photo credit: He Wang and Yuanyuan Hong). (b) An unknown artist's painting of 19th-century Hong Kong (Hong Kong Island and Victoria Harbour in ~1862, adapted from Morton, 2016). (c) Hong Kong population change; data from Evans (2017) and the World Bank.

their names identified by Brady (1869) and on the morphological similarities of those potentially misidentified species to known “correct” species in Hong Kong (Hong et al., 2019, 2022). The species reported by Brady (1869) in the 19th century were then compared to species known in the 21st century in the latest and first comprehensive ostracod survey in Hong Kong, which includes 52 sites covering almost the entire Hong Kong marine area and more than 10 000 ostracod specimens (Hong et al., 2019, 2022).

### 3 Results and discussion

Brady (1869) reported 17 ostracod species from 19th-century Hong Kong (Table 1, Fig. 2). We updated their taxonomic names as shown in Table 1. *Neonesidea*, *Propontocypris*, and *Xestoleberis* are identified at the genus level only because of taxonomic difficulty due to their smooth shells and the resulting paucity of useful morphological characters for species identification. Uncertainties remain for several species. *Cythere cribriformis* Brady, 1866 and *Cythere darwinii* Brady, 1868 are *Pistocythereis cribriformis* (Brady, 1866) and *Ruggieria darwinii* (Brady, 1968), respectively, in the contemporary taxonomy, but there are several morphologically similar species, such as *Pistocythereis bradyformis* (Ishizaki, 1968) and *Pistocythereis bradyi* (Ishizaki, 1968), that were not known or described at that time. In considering the broader species concept in use in the 19th century, there could be the possibility of misidentifications, in our opinion. Two Mediterranean species identified by Brady (*Cythere crispata* Brady, 1868 and *Cythere hodgii* Brady, 1866) are very unlikely to be present in Hong Kong considering the distance and the fact that they were absent in subsequent Hong Kong ostracod studies. We identified them as *Callistocythere* aff. *undulatifacialis* Hanai, 1957 (Hong et al., 2019) and *Keijella kloempritensis* (Kingma, 1948), respectively, based on their morphological similarities. However, some uncertainties are unavoidable in such estimations without illustrations of Brady's original specimens. Indeed, *Cythere hodgii* is also similar to juveniles of *Bicornucythere bisanensis* s.l. (e.g., Abe, 1988; Yasuhara and Irizuki, 2001), and the possibility of misidentification certainly exists. *Aurila cymba* (Brady, 1869) is attributed to *Aurila* sp. 2 of Hong et al. (2019), and we confirmed they are morphologically identical based on the lectotype SEMs in Whatley and Zhao (1988a) and our Hong Kong specimens (Hong et al., 2019) (Fig. 2). *Robustaurila salebrosa* (Brady, 1869) was absent in Hong et al. (2019), but there is a certain possibility that juveniles identified as *Robustaurila* cf. *ishizakii* (Okubo, 1980) by Hong et al. (2019) are juveniles of *Robustaurila salebrosa*. The type specimens of *Loxoconcha hastata* Brady, 1869 that Brady described as a new species from Hong Kong were lost (Whatley and Zhao, 1988a). Hong Kong specimens reported as *Loxoconcha japonica* Ishizaki, 1968 in Hong et al. (2019) are very similar to Brady's original sketches of *Loxoconcha hastata*, but we prefer to keep them as *Loxoconcha japonica* because of the lack of type specimens or SEM images of *Loxoconcha hastata* and the widely used name *Loxoconcha japonica*. Specimens of *Loxoconcha sinensis* Brady, 1869 shown in Whatley and Zhao (1988a) include two species. The lectotype is, of course, *Loxoconcha sinensis* (= *Loxoconcha* cf. *kattoi* Ishizaki, 1968 of Hong et al., 2019), and the paralectotypes are a different species, *Loxoconcha epeterseni* Ishizaki, 1981.

We compared Brady's species presence data (as no abundance is available there) with the top 30 species regarding



**Figure 2.** Scanning electron micrographs of selected ostracod species described or reported by Brady (1869). All specimens are from Hong Kong and from Hong et al. (2019). (1) *Aurila cymba* (Brady, 1869), adult left valve. (2) *Callistocythere* aff. *undulatifacialis* Hanai, 1957 of Hong et al. (2019), adult right valve. (3) *Cytherelloidea cingulata* (Brady, 1869), left valve. (4) *Loxoconcha epeterseni* Ishizaki, 1981, adult male right valve. (5) *Loxoconcha japonica* Ishizaki, 1968, adult female left valve. (6) *Loxoconcha sinensis* Brady, 1869, adult female left valve. (7) *Keijella kloempriensis* (Kingma, 1948), adult left valve. (8) *Neocytheretta adunca* (Brady, 1880), adult right valve. (9) *Sinocytheridea impressa* (Brady, 1869), adult female left valve. See Table 1 for the details and uncertainties regarding identifications of species described or reported by Brady (1869).

the total abundance in Hong et al. (2019) (Tables 1 and 2, Fig. 3). Rather surprisingly, Brady did not report some of today's very abundant species, and, conversely, many of Brady's species are not among the top 30 species in the 21st century. Three out of four species known as pollution-, eutrophication-, or hypoxia-tolerant species (Hong et al., 2019) were not reported by Brady (1869). The well-known eutrophication- and hypoxia-tolerant species and most dominant species in Hong Kong, *Sinocytheridea impressa* (Brady, 1869), was reported and described. On the other hand, the second most dominant species, *Neomonoceratina delicata* Ishizaki and Kato, 1976 (a pollution-tolerant species), and a very abundant species, *Loxoconcha malayensis* Zhao and Whatley, 1989 (a hypoxia-tolerant species), were not reported or mentioned there. Of course, Brady (1869) is a taxonomy paper and does not necessarily report all abundant species. Still, this biased coverage of species suggests the possibility that these tolerant species were less abundant in the 19th century long before the Hong Kong's industrialization, when Hong Kong was not impacted by human activity to a great extent. In contrast, many (not all though) sensitive taxa in this regard (e.g., *Propontocypris*, *Xestoleberis*,

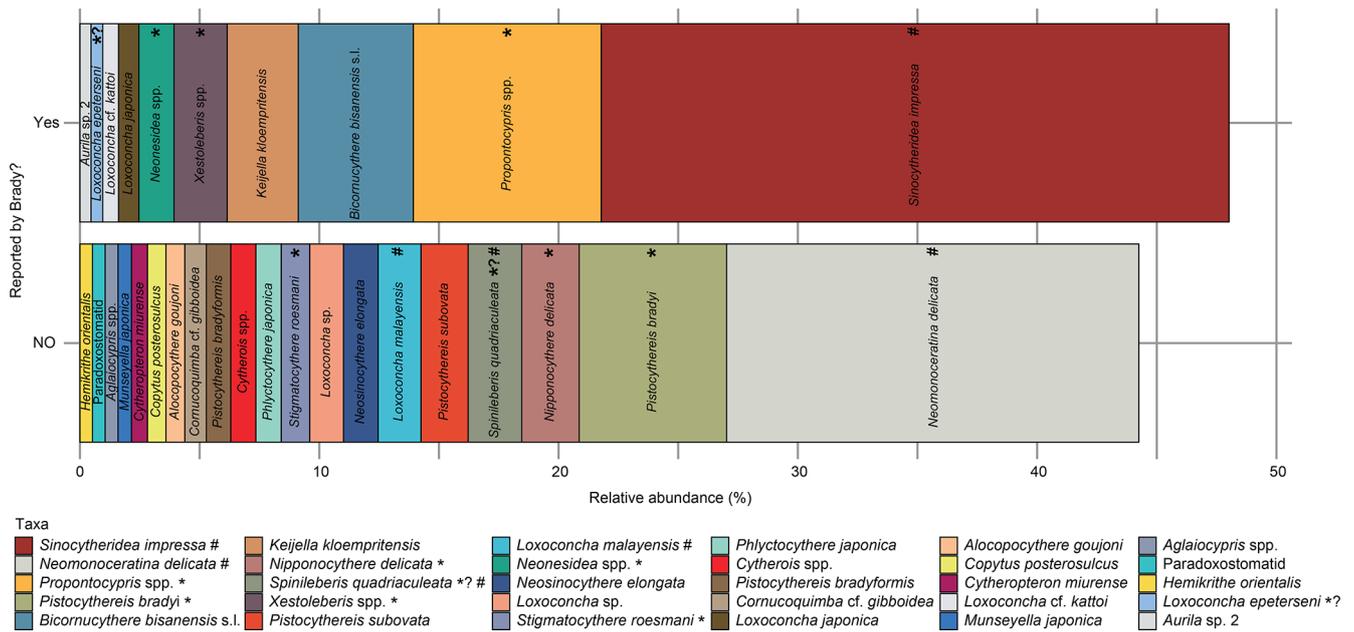
*Neonesidea*) were reported by Brady (1869) in line with this assumption.

Eight species reported by Brady (1869), namely *Bythoceratina orientalis* (Brady, 1869), *Neocytheretta adunca* (Brady, 1880), *Callistocythere* aff. *undulatifacialis*, *Pistocythereis euplectella* (Brady, 1869), *Robustaurila salebrosa*, *Cytherelloidea cingulata* (Brady, 1869), *Pistocythereis cribriformis*, and *Ruggieria darwinii*, are rare (i.e., out of the top 30) or not reported in Hong et al. (2019) (Tables 1 and 2). While some could be misidentification, as discussed above, this biased coverage of now-rare species by Brady (1869) may indicate that the ostracod faunal composition in the 19th century was substantially different from that of the 21st century and that these species were more abundant in the 19th century than in the 21st century. Industrialization-induced pollution, eutrophication, and deoxygenation in Hong Kong may have diminished their occurrence. Also, many of them (e.g., *Neocytheretta adunca*, *Pistocythereis euplectella*, *Cytherelloidea cingulata*, *Pistocythereis cribriformis*, and *Ruggieria darwinii*) are known as tropical species and are reported from the equatorial western Pacific (Whatley and Zhao, 1987, 1988b). Hong Kong sea surface temperatures have decreased since ~1900 AD by ~1–2 °C, at least in the eastern part, due to

**Table 1.** Taxonomic updates of Brady's Hong Kong ostracods (Brady, 1869) and their comparison with the 21st-century ostracod record (Hong et al., 2019) (i.e., whether Brady's species were recoded and within the top 30 species regarding their total abundance in Hong et al., 2019; also see Table 2).

Species by Brady (1869)			Comparison with Hong et al. (2019)	
Names by Brady (1869)	Updates by Whatley and Zhao (1988a)	Names in the present study	Recorded?	Top 30 sp.?
<i>Bairdia elegans</i> (as new species there)	<i>Neonesidea elegans</i> (Brady, 1869)	<i>Neonesidea</i>	Y*	Y*
<i>Bairdia subdeltoidea</i> (von Münster, 1830)		<i>Neonesidea</i>	Y*	Y*
<i>Bythocythere orientalis</i> (as new species there)	<i>Bythoceratina orientalis</i> (Brady, 1869)	Same as Whatley and Zhao	Y	N
<i>Cythere cerebralis</i> Brady, 1868		<i>Neocytheretta adunca</i> (Brady, 1880)	Y?	N
<i>Cythere cribriformis</i> Brady, 1866		<i>Pistocythereis cribriformis</i> (Brady, 1866) but could be misidentification?	N?	N?
<i>Cythere crispata</i> Brady, 1868		<i>Callistocythere</i> aff. <i>undulatifacialis</i> Hanai, 1957 of Hong et al. (2019)?	Y	N
<i>Cythere cymba</i> (as new species there)	<i>Aurila cymba</i> (Brady, 1869)	<i>Aurila cymba</i> (Brady, 1869) (= <i>Aurila</i> sp. 2 of Hong et al., 2019)	Y	Y
<i>Cythere darwinii</i> Brady, 1868		<i>Ruggieria darwinii</i> (Brady, 1868) but could be misidentification?	N?	N?
<i>Cythere euplectella</i> (as new species there)	<i>Lankacythere euplectella</i> (Brady, 1869)?	<i>Pistocythereis euplectella</i> (Brady, 1869)	Y	N
<i>Cythere hodgii</i> Brady, 1866		<i>Keijella kloempritensis</i> (Kingma, 1948) or juvenile of <i>Bicornucythere</i>	Y	Y
<i>Cythere salebrosa</i> (as new species there)	<i>Mutilus salebrosa</i> (Brady, 1869)	<i>Robustaurila salebrosa</i> (Brady, 1869)	N	N
<i>Cytherella cingulata</i> (as new species there)	<i>Cytherelloidea cingulata</i> (Brady, 1869)	Same as Whatley and Zhao (1988a)	Y	N
<i>Cytheridea impressa</i> (as new species there)	<i>Sinocytheridea impressa</i> (Brady, 1869)	Same as Whatley and Zhao (1988a)	Y	Y
<i>Loxoconcha hastata</i> (as new species there)	Brady's specimen lost	<i>Loxoconcha japonica</i> Ishizaki, 1968?	Y?	Y?
<i>Loxoconcha sinensis</i> (as new species there)	<i>Loxoconcha sinensis</i> Brady, 1869	<i>Loxoconcha sinensis</i> Brady, 1869 (= <i>Loxoconcha</i> cf. <i>kattoi</i> in Hong et al., 2019), <i>Loxoconcha epeterseni</i> Ishizaki, 1981	Y	Y
<i>Pontocypris davisoni</i> Brady, 1868		<i>Propontocypris</i>	Y*	Y*
<i>Xestoleberis aurantia</i> (Baird, 1838)	<i>Xestoleberis hanaii</i> Ishizaki, 1968	<i>Xestoleberis</i>	Y*	Y*

\* Genus level.



**Figure 3.** The top 30 ostracod taxa regarding total abundance in the 21st-century survey (Hong et al., 2019), divided into two groups: taxa reported by Brady (1869) (Group Yes) and those not reported (Group No). Their indicator statuses also indicated (i.e., sensitive (\*)/tolerant (#) to pollution, eutrophication, or deoxygenation); also see Table 2.

enhanced upwelling related to the East Asian summer monsoon intensification (Kong et al., 2015). This temperature decline would be unfavorable for the tropical species in subtropical Hong Kong. In contrast, some temperate species, such as *Pistocythereis bradyi*, *Nipponocythere delicata*, and *Spinileberis quadriaculeata* (Brady, 1880) (Yasuhara and Seto, 2006; Hong et al., 2019), that are very abundant in the 21st century were not reported by Brady (1869) (Table 2, Fig. 3), suggesting that the temperature decline was favorable for the temperate species in subtropical Hong Kong. The temperature decline over the last ~100 years might have affected the abundance of these tropical and temperate species negatively and positively, respectively, in subtropical Hong Kong.

In summary, inconsistencies between species covered by a 19th-century taxonomy paper and those abundant in a 21st-century survey indicated the possibility that the 19th-century ostracod fauna under much less polluted and ~1–2 °C warmer conditions were substantially different to those in the present day. There is an uncertainty in the exact position of the studied locality by Brady (1869) (apart from being in Hong Kong); thus further detailed comparison, e.g., with nearby sites in Hong et al. (2019), is impossible, while future exploration of museum collections and archives may give us more precise information. At the same time, it is unlikely that possible differences in water depths between the sites of Brady (1869) and Hong et al. (2019) affect our results because most of Hong Kong's marine areas are quite shallow, < 20–30 m. Historical ecology is a powerful tool

to detect human- and climate-induced long-term changes in marine communities. Last but not least, natural history museums that house historical collections of specimens sustainably and permanently are essential for historical ecology, as this study was impossible without such specimens and their restudy by Whatley and Zhao (Whatley and Zhao, 1988a; Zhao and Whatley, 1988).

**Data availability.** Data are shown in Tables 1 and 2.

**Sample availability.** No samples were used in this article.

**Author contributions.** MY conceived and designed the research. MY and YH carried out the research and analyses. MY wrote the paper with contributions from YH.

**Competing interests.** At least one of the (co-)authors is a member of the editorial board of *Journal of Micropalaeontology*. The peer-review process was guided by an independent editor, and the authors also have no other competing interests to declare.

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**Table 2.** The top 30 ostracod taxa regarding total abundance in the 21st-century survey (Hong et al., 2019), their indicator statuses (sensitive/tolerant to pollution, eutrophication, or deoxygenation), and their status (i.e., reported or not) in Brady (1869). Brady's species below the top 30 of Hong et al. (2019) are listed at the bottom of the table.

Taxa	Total abundance	% abundance	Sensitive	Tolerant	In Brady (1869)?
<i>Sinocytheridea impressa</i> (Brady, 1869)	3404	26.24		#	Y
<i>Neomonoceratina delicata</i> Ishizaki and Kato, 1976	2235	17.23		#	N
<i>Propontocypris</i> spp.	1018	7.85	*		Y
<i>Pistocythereis bradyi</i> (Ishizaki, 1968)	799	6.16	*		N?
<i>Bicornucythere bisanensis</i> s.l. (Okubo, 1975)	624	4.81			Y?
<i>Keijella kloempritenensis</i> (Kingma, 1948)	385	2.97			Y?
<i>Nipponocythere delicata</i> Ishizaki and Kato, 1976	312	2.40	*		N
<i>Spinileberis quadriaculeata</i> (Brady, 1880)	290	2.24	*?	#	N
<i>Xestoleberis</i> spp.	288	2.22	*		Y
<i>Pistocythereis subovata</i> Gou in Gou et al., 1983	256	1.97			N?
<i>Loxococoncha malayensis</i> Zhao and Whatley, 1989	232	1.79		#	N
<i>Neonesidea</i> spp.	191	1.47	*		Y
<i>Neosinocythere elongata</i> (Hu, 1976)	188	1.45			N
<i>Loxococoncha</i> sp.	183	1.41			N
<i>Stigmatocythere roesmani</i> (Kingma, 1948)	154	1.19	*		N
<i>Phlyctocythere japonica</i> Ishizaki, 1981	137	1.06			N
<i>Cytherois</i> spp.	136	1.05			N
<i>Pistocythereis bradyformis</i> (Ishizaki, 1968)	132	1.02			N?
<i>Cornucoquimba</i> cf. <i>gibboidea</i> (Hu, 1982)	117	0.90			N
<i>Loxococoncha japonica</i> Ishizaki, 1968	110	0.85			Y?
<i>Alocopocythere goujoni</i> (Brady 1868)	103	0.79			N
<i>Copytus posterosulcus</i> Wang in Zhao et al., 1985	100	0.77			N
<i>Cytheropteron miurense</i> Hanai, 1957	87	0.67			N
<i>Loxococoncha</i> cf. <i>kattoi</i> , Ishizaki 1968	85	0.66			Y
<i>Munseyella japonica</i> (Hanai, 1957)	73	0.56			N
<i>Agelaiocypris</i> spp.	70	0.54			N
Paradoxostomatid	69	0.53			N
<i>Hemikrithe orientalis</i> van den Bold, 1950	67	0.52			N
<i>Loxococoncha epeterseni</i> Ishizaki, 1981	63	0.49	*?		Y
<i>Aurila</i> sp. 2	60	0.46			Y
Taxa not in the top 30 of Hong et al. (2019) but reported by Brady (1869)					
<i>Bythoceratina orientalis</i> (Brady, 1869)					
<i>Neocytheretta adunca</i> (Brady, 1880)					
<i>Callistocythere</i> aff. <i>undulatifacialis</i> Hanai, 1957					
<i>Pistocythereis euplectella</i> (Brady, 1869)					
<i>Robustaurila salebrosa</i> (Brady, 1869)					
<i>Cytherelloidea cingulata</i> (Brady, 1869)					
<i>Pistocythereis cribriformis</i> (Brady, 1869)? (could be misidentification; see text)					
<i>Ruggieria darwinii</i> (Brady, 1868)? (could be misidentification; see text)					

ery effort to include appropriate place names, the final responsibility lies with the authors.

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