The pygmy right whale, *Caperea marginata*, is the last of the cetotheres.

The pygmy right whale, *Caperea marginata*, is the smallest, most cryptic and least known of the living baleen whales (Mysticeti). Little is known of *Caperea* in terms of musculoskeletal functional systems, feeding and social behaviour, and distribution in relation to oceanic conditions [1]. *Caperea* thus contrasts sharply with other living species of baleen whales (in families Balaenidae, Eschrichtiidae and Balaenopteridae), whose biology is much better known from direct observation of living, stranded and captured individuals. Infrequent strandings of mainly single *Caperea*, and the dearth of sightings, suggest cryptic and semi-solitary habits around the Southern Ocean, yet large pelagic clusters of individuals have been reported [1]. Early records of the species were based on beach-cast fragments in the mid-1800s, producing a complex history of names that led to the present use of *C. marginata* [2,3]. From the beginning, the pygmy right whale has been known for its unusual skeletal form (figure 1) [4], and indeed its skeletal disparity explains why the species is the sole member of one (Neobalaenidae) of the four families of living mysticetes [2,4–6].

In spite of its common name, the pygmy right whale differs from right whales (Balaenidae) in its external form and osteological features in all parts of the skeleton [1,4]. Indeed, despite concentrated recent research on the phylogenetics of mysticetes [7–15], the evolutionary relationships of *Caperea* have remained largely elusive. Molecular and morphological studies have regularly championed markedly different hypotheses, allying *Caperea* either with rorquals (Balaenopteridae) on the basis of molecular evidence [9–11], or right whales on the basis of morphology [7,8,12–14]. Controversy over relationships has been compounded by a lack of published reports of unambiguous fossil neobalaenids (which might otherwise provide hard evidence of ancient evolutionary history) [16–18], the relative scarcity of specimens of *Caperea* in Northern Hemisphere natural history collections, and what we interpret as the likely evolutionary convergence of the feeding apparatus with that of right whales.

The wealth of material housed in New Zealand collections, ranging from neonate and stillborn calves to mature individuals, provides an opportunity to amend this situation. Detailed observations and comparisons revealed a series of ontogenetically variable and phylogenetically significant features previously unreported in...
Caperea (figures 1 and 2; see also the electronic supplementary material), including some in the feeding apparatus (the juvenile presence of a well-developed, parallel-sided ascending process of the maxilla, and a well-developed, long and low coronoid process on the mandible) and in the ear region (a reduced caudal tympanic process and the presence of a large, hypertrophied, shelf-like lateral tuberosity of the periotic). Among mysticetes, Caperea shares the latter two ear features exclusively with members of the fossil subfamily Herpetocetinae [19], in turn a subdivision of the reportedly extinct Cetotheriidae sensu stricto [7,8,15] (hereafter, Cetotheriidae is used in this sense). Interestingly, these observations add to a range of other similarities between Caperea and cetotheres, including the presence of a hypertrophied, conical compound posterior process of the tympanoperiotic, a poorly developed conical process of the tympanic bulla, pointed nasals and a well-developed sagittal crest on the supraoccipital, thus hinting at the entirely novel possibility of a an evolutionary relationship between these superficially different taxa. In this study, we test whether these similarities might indicate an evolutionary link between Caperea and cetotheres, by assessing them within a broader phylogenetic framework.

Figure 1. Comparison and shared features of the skulls of (a,b,e) the living pygmy right whale Caperea marginata (Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand, MM002235) and (c,d,f) the extinct cetothere Herpetocetus transatlanticus (United States National Museum of Natural History, Washington DC, USA, 182962) in (a,c) dorsal, (b,d) ventral and (e,f) posterior views.
2. Material and methods

We constructed an illustrated morphological data matrix of 23 taxa and 166 unordered osteological characters (MorphoBank project 578), drawing on several previously published analyses [7–9,12–15]. To test the effect of morphological versus molecular data, we combined our dataset with the molecular dataset of McGowen et al. [10]. Taxa were chosen so as to represent all major mysticete families and cover as much of their temporal range as possible, ranging from archaic, via relatively recently extinct, to extant. Thus, in addition to a well-sampled Cetotheriidae, our matrix includes living representatives of all of the extant families, as well as the oldest undisputed balaenid (Morenocrinus parvus [20]) two of the oldest known balaenopterids (‘Megaptera’ niucaena [21] and Plisobalaenoptera guartrelli [22]) and a range of other balaenids and balaenopteroids. The extinct archaeocete Zygorhiza lachii and the extant sperm whale Physeter macrocephalus were chosen as outgroups.

We performed two separate analyses: (i) a parsimony-based analysis of the morphological data only; and (ii) a Bayesian total evidence analysis including both molecular and morphological data. For the morphological analysis, branch support was assessed through Bremer support values [23], as well as symmetric resampling (2000 replicates), recorded as GC values [24]. Full details of the cladistic methodology employed here are provided in the electronic supplementary material.

3. Results

The results of the two analyses were similar (figure 3; electronic supplementary material), and confirmed previous molecular studies in finding Caperea to form a well-supported clade with balaenopterids and eschrichtiids, rather than with balaenids (right whales). In terms of morphology, this solution was seven steps shorter than one enforcing the long-held morphological view of a clade comprising Cetopera and balaenids [6–8,12–14]. Living mysticetes fell into three mostly well-supported clades: (i) a monophyletic Balaenidae; (ii) balaenopteroids, including several hitherto supposed ‘cetotheres’ [7,19], Eschrichtius robustus and the living balaenopterids; and (iii) a monophyletic Cetotheriidae, including C. marginata. Within cetotheres, Caperea was most closely related to a herpetocetine clade [8,19], comprising Herpetocetus and Nannocetus.

Caperea unequivocally shares with herpetocetines a continuous lateral skull border (char. 42); a triangular and ventromedially oriented postglenoid process (chars. 63, 65); a postglenoid process located in line with the anterior half of the tympanic bulla (char. 77); an irregular, L-shaped anterior edge of the anterior process of the periocrist (char. 85); a broad, elongate, shelf-like lateral tuberosity of the periocrist articulating with the squamosal (char. 92); a flattened ventral surface of the periocrist (char. 94); a greatly reduced caudal tympanic process of the periocrist (char. 98); and a low conical process of the tympanic bulla (char. 120) (figures 1 and 2). Caperea, furthermore, shares with both Piscobalaena and herpetocetines the presence of anteriorly pointed and sagittally keeled nasals (chars. 38, 39), and with all cetotheres except Cetotherium the presence of a strikingly conical, plug-like compound posterior process of the tympanoperiotic (char. 110). Finally, Caperea shares with all cetotheres the presence of a ridge-like parieto-squamosal suture (char. 59); reversed in Herpetocetus), as well as a posterior process of the tympanoperiotic broadly exposed on the lateral skull wall (char. 111).
molecular phylogenies; and (iii) closing the gap between the living pygmy right whale and its assumed early divergence during the Early Miocene.

Based on these shared features and our cladistic analysis, we therefore refer Caperea marginata to Cetotheriidae, retaining Neobalaeninae as a subfamily in recognition of the disparate morphology of Caperea relative to other cetotheres:

Cetacea Brisson, 1762
Mysticeti Gray, 1864
Cetotheriidae Brandt, 1872; resurrected from extinction
Neobalaeninae Gray, 1873; new rank.

4. Discussion and conclusions

Our results for the first time place Caperea conclusively in a broader evolutionary framework and resolve several problems that have vexed the systematics of this whale to date. Previous morphological analyses [7,8,12–14] emphasized anatomical similarities of Caperea with right whales (Balaenidae). Such comparisons contradict molecular interpretations, and further, in the absence of almost any Caperea-like fossils (but see [16]), imply a surprisingly long ghost lineage for Caperea from the earliest Miocene, at least 20 Ma (based on the oldest described balaenid, M. parvus) [20]. Molecular results have also pointed to an early divergence date for Caperea, Miocene–Oligocene in the range of 17.6–26 Ma [10,11] but, unsurprisingly, have not identified likely fossil relatives of the pygmy right whale. Our analysis now resolves all these issues by (i) reconciling morphological and molecular phylogenies; (ii) identifying cetotheres as previously unrecognized fossil relatives (including sister taxa) of Caperea; and (iii) closing much of the gap between the living pygmy right whale and its assumed early divergence during the Early Miocene or Late Oligocene.

The oldest reliable records of the Caperea–cetotheriid clade are Cetotherium nathkii and Joumocetus shimizu, both probably dating to the Early Tortonian (9.4–11.6 Ma; see the electronic supplementary material) [25,26]. Metopocetus durinassus may be even older, dating to the Langhian (13.8–16 Ma), but there is some uncertainty as to which formation the only known specimen (aff. Herpetocetus) dating to the Langhian has been reported from northern Baja California,
Mexico, but has yet to be described [27]. The reported Langhian records of Cetotheriidae fall within the 99 per cent highest posterior distribution ranges of some recent molecular clock studies [10], despite being at least 2–10 Myr younger than all previously proposed molecular divergence estimates for Caperea. Because both M. durinasus and Herpetocetus show several disparate and derived characters, such as a conical compound posterior process of the tympanoperiosteum, we expect that Cetotheriidae had a substantial earlier history, and that new finds will extend the record of cetotheres closer to the estimated molecular split of Caperea from other living baleen whales.

Within Cetotheriidae, the oldest occurrence of Nannocetus eremus from the Late Miocene (approx. 9 Ma) of California (electronic supplementary material) provides a minimum age estimate for the divergence of Caperea from other cetotheres (figure 3). The virtual absence of described Caperea-like fossils (but see [16]) from the otherwise relatively well-sampled interval of 0–9 Ma could reflect a largely austral distribution of the clade, as for the living pygmy right whale. Compared with the Northern Hemisphere, the austral record of Late Miocene and Pliocene cetaceans is extremely patchy, and mainly limited to fossils from South America [7,12,18]. We therefore expect that fossil relatives of Caperea will be found through increased sampling of the Neogene of South America, Africa and Australasia.

Despite the similarities highlighted by our study, a morphological gulf remains between Caperea and other cetotheres, which is likely to be related to fundamentally different feeding strategies. It is not inconceivable that the larger size and superficially balaenid-like skull architecture of Caperea may have helped it to survive the Pliocene demise of the last of its cetothere relatives. Given the patchy fossil record, there is presently no evidence as to when the ecomorphological divergence of neobalaenines from other cetotheriids is likely to have started, or indeed what might have driven it. Insight from the living species, such as the recent discovery of visual pigment-associated deep-diving behaviour in Caperea [28], might hold potential clues, but any further analyses of these issues will have to await the description of more informative fossil material.

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