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Review Article

Efficacy of Cryptic rodents and challenges for conservation in Africa: A review

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Abstract

Cryptic species are unique species that are genetically divergent, although formerly nominated as a single species because of their morphological indistinguishability. In the last 20 years, it has been widely documented as a cryptic species in scientific articles and has nearly consistently dispersed across all taxa and ecological niches. Unfortunately, the inconsistency of cryptic species' descriptions and taxonomic classification makes it difficult to quantify and understand their coevolutionary relevance and ecological questions. We aim to review the cryptic rodent species, discuss the mechanisms to describe them, the reasons how diversified, and assess their challenges for conservation. From a limited review of the literature, we found significant numbers of cryptic putative rodent species on the African continent. Methodological error, evolution processes, mutation, speciation, morphological homology, and convergence might be associated with cryptic species. Our regression analysis shows that cryptic species are distributed almost evenly across almost all rodent families in almost all countries. The scatterplot analysis indicates cryptic diversity has a linear scale associated with the number of publications and time. Our result shows articles emphasized the importance of molecular, morphological, cytogenetic, and ecological niche approaches in understanding crypticity. An integrated approach is more appropriate to recognize and decode the notions of cryptic nature, notably for divers' small mammals, rather than using single methods. Understanding cryptic species is crucial for exact biodiversity estimation and conservation, including endemic and endangered species.

Keywords: Conservation, Cryptic species, Molecular, Morphology, Rodent

Introduction

Cryptic species are multiple distinct taxa that were nominated as a single species due to morphological indistinguishability, but they are genetically unique (Paterson, 1991; Lincoln, 1998; Wellborn and Cothran, 2004; Corti *et al*., 2005; Stuart *et al*., 2006; Bickford *et al*., 2007; Pfenninger and Schwenk, 2007; Ceballos and Ehrlich, 2009; Trontel and Cene, 2009; Oliver *et al*., 2010; Morard *et al*., 2016; Chenuil *et al*., 2019; Egea *et al*., 2019; Daly *et al*., 2021). They are complex and have many reproductively distinct lineages (Knowlton, 1993; Lincoln, 1998; Mayr, 1999; Witt *et al*., 2006; Bickford *et al*., 2007; Oliver *et al*., 2010; Lee and Oliver, 2016). These concepts are more in modern biodiversity studies (Bickford *et al*., 2007). Although it has been around for several hundreds of years (Mayr, 1942; Winker, 2005; Bickford *et al*., 2007; Pfenninger and Schwenk, 2007). The cryptic reports were started in 1718 in the avian genus *Phylloscopus* and have exponentially increased in publications since around 1986 (Wilson and Reeder, 2005). Due to the increase of researchers in the field and the applications of molecular advancements. Numerous factors contribute to the cryptic species' existence: methodological error; morphological diagnostic methods alone lead to misidentification of hidden and putative cryptic species (morphologically indistinguishable) (Paterson, 1991; Knowlton, 1993; Lincoln, 1998; Mayr, 1999; Saez and Lozano, 2005; Winker, 2005; Witt et al., 2006; Bickford *et al*., 2007; Pfenninger and Schwenk, 2007; Ceballos and Ehrlich, 2009; Oliver *et al*., 2010; Nygren and Pleijel, 2011;Jorger and Schrodl, 2013; Lee and Oliver, 2016; Struck *et al*., 2018). However, there is difficulty in understanding the core components of biodiversity, which are genes, species, and their ecological relationships (Mayden, 1997; de Queiroz, 1998; 2005; Fiser *et al*., 2018). In particular, there is no direction or threshold on how morphologically analogous species should be or how many characters should differ in order to be considered cryptic.

There are many reasons why cryptic species exist; methodological error; morphological diagnostic methods alone lead to misidentification of hidden and putative cryptic species (morphologically indistinguishable) (Eme *et al*., 2018; Fiser *et al*., 2018; Theodoridis *et al*., 2019). Morphological convergence, divergence, and niche conservatism, are also major reasons (Trontelj and Cene, 2009; Fiser *et al*., 2018; Struck *et al*., 2018). Morphological homology is linked with the morphological convergence (Trontelj and Cene, 2009; Bravo *et al*., 2014; Fiser *et al*., 2018). The continuous evolution of morphologically distinct ancestors produces morphological homology (Struck *et al*., 2018). In addition to divergence theory, cryptic species have recently diverged, with significant morphological distinction (Egea *et al*., 2016; Fiser *et al*., 2018). Morphological divergence and disparity increased through time (Harmon *et al*., 2003; Adams *et al*., 2009; Zúñiga-Reinoso and Benítez, 2015; Struck *et al*., 2018). Continuous and lack of morphological variations across time (Mayr, 1942; De Queiroz, 2007; Gómez *et al*., 2002; Singhal *et al*., 2018). Descendants exhibition phenotypic change over the years, offering a unique chance to investigate adaptation processes responsible for morphological conservation across historical time frames (Smith *et al*., 2011). Sibling taxa or complexes that maintain a high level of morphological identity across time are referred to be cryptic species (Struck *et al*., 2018). Ecological flexibility also determines morphogenesis by shifting abiotic restrictions (Trontelj and Cene, 2009). Niche conservatism also argues that competition constrains causes for niche change and morphological divergence among descendant species, and phenotypic stagnation (Trontelj and Cene, 2009; Smith *et al*., 2011; Egea *et al*., 2016). The existence of speciation across taxa (Winger and Bates, 2015). Mutations cause speciation, reduced mating across parental units, and decreased hybrid fitness (Rabosky and Matute, 2013). Speciation is a genetic phenomenon, and genetic data is what defines the classification of cryptic class (Baker, 1984).

Health, agriculture, and fish management issues are raised as the major challenges due to the presence of obscure taxa (Corti *et al*., 2005; Bickford *et al*., 2007⁝ Baskevich *et al*., 2016). Overestimation of a species' geographic range and environmental change (Egea *et al*., 2016; Eme *et al*., 2018; Chenuil *et al*., 2019). However, the reality of obscure species has numerous reimbursements, such as taxonomic connections, ecological and macroevolutionary processes such as speciation, convergences, and stasis (Mayr, 2013; Struck *et al*., 2018). Moreover, continuing accounts of cryptic diversity have a great influence on biodiversity estimations and conservation management concerns (Trontelj and Cene, 2009; Smolensky, 2014; Skoracka *et al*., 2015; Morard *et al*., 2016; Chenuil *et al*., 2019; Korshunova *et al*., 2019). Many concerns have raised as a result of their rapid discovery, such as: how common are cryptic species? Do cryptic creatures have a recent evolutionary history? Besides that, are there more cryptic species in tropical biomes than in temperate biomes? Which animal taxon has the largest number of new species? Cryptic have been listed and introducing them as sibling species exposes them to morphological complications and reproductive separation of taxon groups (Saez and Lozano, 2005). They are widespread and common in all animal phyla (Hebert *et al*., 2004; Pfenninger and Schwenk, 2007; Adams *et al*., 2014; Fennessy *et al*., 2016; Perez-PoncedeLeo and Poulin, 2016; Korshunova *et al*., 2019; Daly *et al*., 2021). However, it is difficult to understand their concepts, taxonomic nomenclature, modifications, and terminology, which also make it difficult to draw firm conclusions about their distribution, nature, and their implications for ecology and evolution (Struck *et al*., 2018). They cause uncertainty in terms of definition, taxonomy, evolution and operational identification (Bickford *et al*., 2007; Struck *et al*., 2018), and distinct species are considered as one.

Rodents are the most diverse, accounting for around 2,590 species globally (van Wilgen,, 2018; Hamilton and Leslie, 2021). Of these, 463 species are found in Africa (Happold, 2013; Monadjem *et al*., 2015; van Wilgen, 2018). It is more than Europe's (Myers, 1998; Myers *et al*., 2000; Amori *et al*., 2011). Recently, over 2000 new species were identified, but they are morphologically indistinguishable and pose real challenges (Galan *et al*., 2012). Of the new identified species, 60% of them are cryptic (Ceballos and Ehrlich, 2008). Over 250 cryptic are mammals (Pfenninger and Schwenk, 2007; Perez-PoncedeLeo and Poulin, 2016). Several experts confirm that rodents in the region are subjected to systematic taxonomic disorder and uncertainty and conflicting (Bekele *et al*., 1993; Capanna *et al*., 1996; Ducroz *et al*., 1997; Fadda *et al*., 2001; Corti *et al*., 2005). Over 100 rodents have incomplete conservation status and many of them are critically endangered (van Wilgen, 2018). They are untouched and undescribed, especially due to the existence of cryptic species, and are badly understood (Ceballos and Ehrlich, 2008; Bryja *et al*., 2019). For instance, around 40 (41.6%) rodent species are cryptic in Ethiopia; they remain undescribed in previous reports (Bryja *et al*., 2019). Many cryptic species are still being overlooked (Bickford *et al*., 2007; Ceballos and Ehrlich, 2008) across the continent because of many reasons. Unlike other vertebrates, they are forgotten in conservation priority program in biodiversity hotspot regions (Amori *et al*., 2011). The increasing destruction and degradation of natural ecosystems also aggravates and leads to extinctions of species (Brooks *et al*., 1999; Laurance, 1999; Brook *et al*., 2003; Brook *et al*., 2006; Sodhi and Brook, 2006). Especially in Afromontane, which is facing conservation challenges (Kuper *et al*., 2004; Ceballos and Ehrlich, 2006; Demos *et al*., 2014). Cryptic animal survive as small, isolated, inbreeding depression, genetic loss, and increased threatened and extinction risks (Struck *et al*., 2018).

Understanding cryptic complexity and existence and their interactions, evolutionary theory, and challenges has significant implications for future conservation management (Blaxter, 2004; Witt *et al*., 2006; Fiser *et al*., 2018), especially for endemic and rare species. In addition, focusing on such biodiversity issues may increase concerns for the future, particularly for diversified and small mammals. From this perspective, we analyzed cryptic rodent studies on their distribution's methods of detection, challenges, and conservation implications.

Material and methods

This review used a comprehensive literature search and synthesis of relevant publications as its methodological strategy. A review article focused on the distributions of cryptic rodent species on a continent, their distribution, challenges, and conservation. The research articles are more related to cryptic species and their distribution ecologically and among the animal taxa. We also evaluated morphological and molecular technique-based articles and comparison-based articles that were assessed systematically. We used; ResearchGate, Web of Science, springer Scopus (http://www.scopus.com), Google Scholar, and university dissertation online library publication reports. The review process was further complemented by searching the relevant articles using the following themes: cryptic, sibling, title, keywords (abstract), unclear, circle, new species, threats of cryptic species, conservation of cryptic species, neglected species, putative species, biodiversity, species complex, molecular and population genetics (DNA, full genome, cytb, nuclear DNA), morphological identification techniques, delimitation, DNA barcoding, phylogeny, phylogeography, and cryptic and their challenges. This was done by employing cryptic rodent species in Africa (1170). We also looked cryptic studies were detected among the metazoans (Fig.4). We collected this literature between September 1, 2021 and March 30, 2022. The screed articles focused on the reviewed organisms; abstracts; aims; methods applied for delimitations and cryptic rodent species restricted studies on the reviewed organisms. We also used Download occurrences GBIF to indicate the distribution of the representative cryptic rodent species (Fig. 8). The articles were checked and duplicated literature was removed using Mendeley Desktop software. A total of 71 articles were filtered and reserved for further analysis, particularly focusing on their methods and distribution. In this review, we also narrate the challenges and reasons for increasing crypticity and their implications for conservation based on 12 peer-reviewed articles. We used several online articles, published journals, and a 2004 IUCN report to determine the described number of rodent species. We analyzed the cryptic distribution per publication and their distribution across the genus from the reviewed articles using R-software 4.1.3 and an excel spreadsheet.

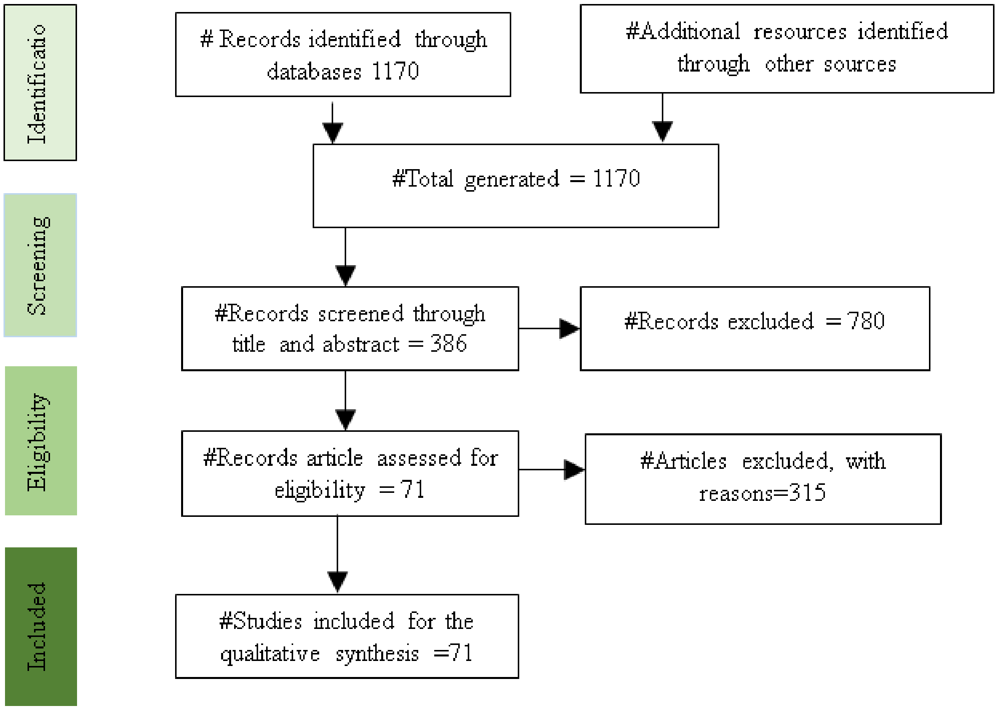

Figure 1. A flowchart for selecting eligible studies on the status of cryptic rodent species on the African continent

Results and discussion

Among 71 eligible articles, which are restricted to a continent, 57 species were nominated as cryptic, belonging to four families and 17 genera (Fig. 1,2). We analyzed the species distribution across the family and genus, as well as the mechanisms of methods to delimit species and challenges. A significant number of described cryptic species were recorded from the limited published articles and families. Of our reviewed from the described rodent species, 27.01% of them are considered cryptic. We observed that the Muridae family had a high number of cryptic species, almost evenly distributed across each genus. The distribution map of the representative cryptic rodent species indicates that they are found in almost every country on the continent of sub-Sahara Africa (Fig. 7). However, cryptic rodent species are more well and frequently described in South and Northern Africa; this may be due to the level of research investigation, but in most areas, particularly in the Afromontane regions, these species are untouched. Simultaneously, we reviewed additional reports on the distributions of cryptic species, which revealed that a large number of cryptic species were observed in all families, sub-families, vertebrates, invertebrates, and classes (Fig. 4. The number of cryptic reporting species many pieces of evidence show that the magnitudes of cryptic were found in all animal taxa including large mammals and continents (Pfenninger and Schwenk, 2007; Perez-PoncedeLeo and Poulin, 2016; Struck *et al*., 2018). We also discussed the diversity of cryptic species in other vertebrate and invertebrate phyla, with significant diversity in all animal group (Fig. 4). In particular, the sub-tropical African geographical area had the highest cryptic diversity of any geographical area next to the neotropics (Pfenninger and Schwenk, 2007). The cryptic species' discovery is not limited to small mammals, but also in large conspecific mammals, including African Wolf (*Canis aureus lupaster*) (Rueness *et al*., 2011; 2015), giraffe species (Fennessy *et al*., 2016), and Ethiopian long- eared bat (genus *Plecotus*) (Ceballos and Ehrlich, 2009) in continent. However, these important aspects of biodiversity are being ignored, which poses challenges for conservation and maybe even raises the possibility of zoonotic reservoir risk (Jorger and Schrodl, 2013). The majority and frequency of cryptic rodent specFies were discovered in South Africa and Northern African countries. The taxa species' evolutionary histories were shaped by persistent climatic oscillation diverse ecology and tectonic evolution. For instance, the trends in genetic proliferation and divergence of cryptic and desert African Jerboas significantly affected geographical and biological processes (Moutinho *et al*., 2020). Cryptic species are the main components of biodiversity and, like the Caucasian rodent species, are the driving forces behind the process of species evolution and speciation (Baskevich *et al*., 2016).

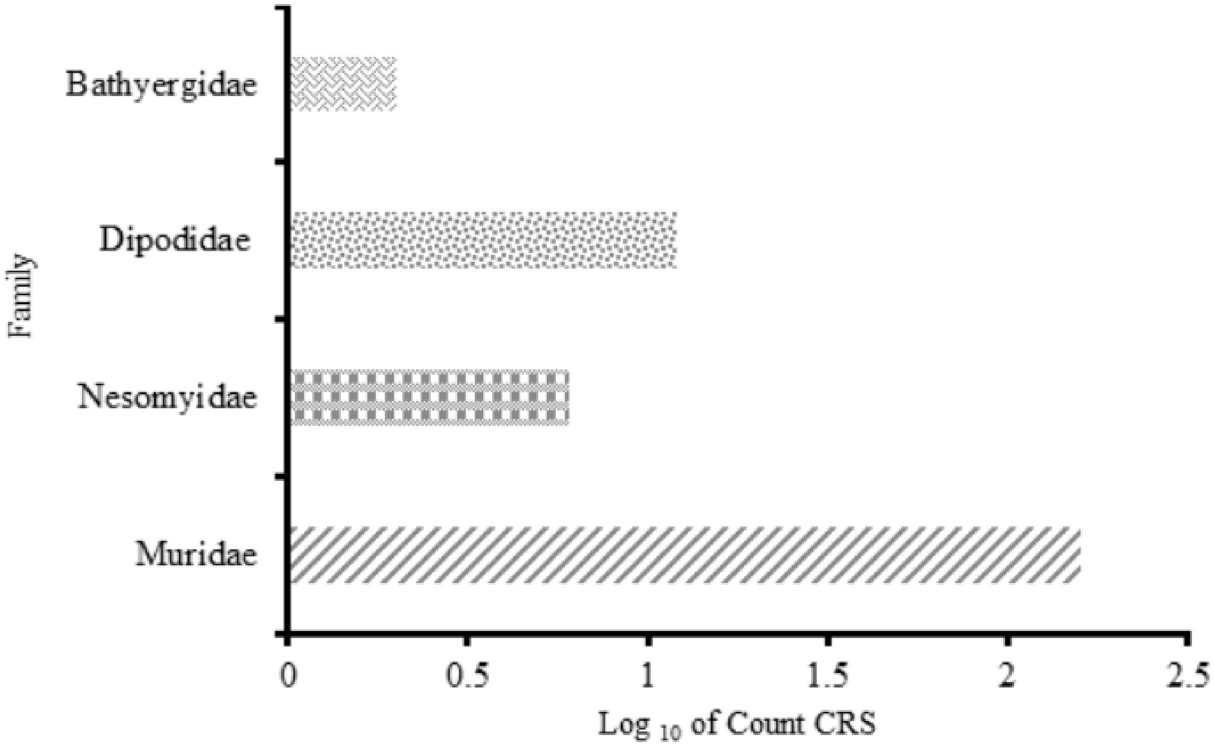

Figure 2. Log $_{10}$ counts putative cryptic species along the described rodent family

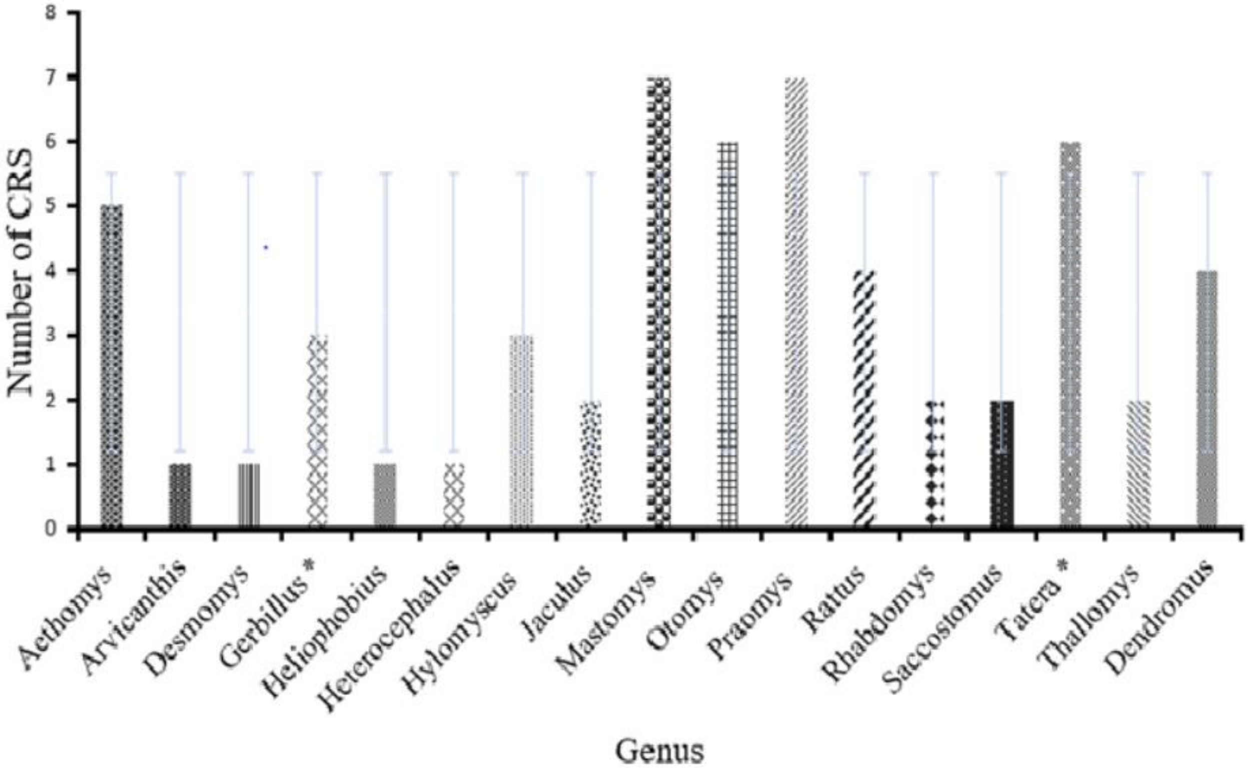

Figure 3. Number of cryptic species aross the described gennus

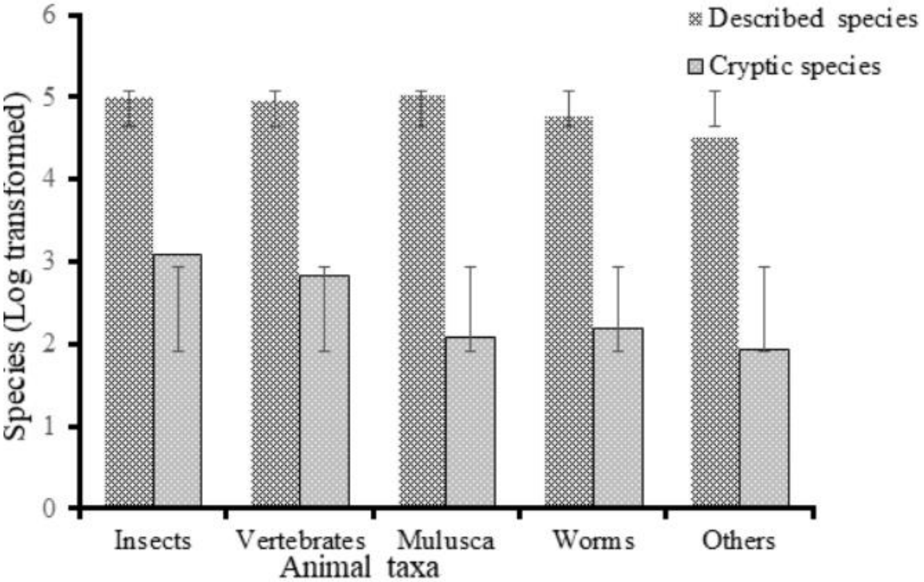

Figure 4. Findings from various literatures on the distribution of cryptic species across continents

The log $_{10}$ number CRS were highly associated with the log $_{10}$ of are described number of species taxonomic family or groups ($Y=0.3286 + 1.1738*X$ $R^2 = 0.4547$, $F_{1.15} = 14.34$, $P = 0.001791$) (Fig. 3). The quantity of cryptic species detected and the number of published article reports have linear scale proportions over time (Fig. 2). There have been a considerable number of publications and meta-analysis reports issued over time about cryptic species diversity, which indicates studies and the magnitude of taxa linear association with them (Pfenninger and Schwenk 2007; Perez-PoncedeLeo and Poulin, 2016; Struck *et al.*, 2018). The results indicate a significant increase in the discovery of cryptic species over time, particularly from 2000 to around 2015 (Figure 5). Note all the methodological factors affect the discovery of the cryptic species. Molecular techniques, like mitochondrial DNA sequencing as well as karyotyping, are effective for discovering cryptic species due to their ability to reveal hidden diversity and differentiate closely related organisms (Bickford et al 2007). Furthermore, the rise in reports of cryptic species over time can be attributed to inadequate species surveys and discrepancies in the identification of previous findings. The increased discoveries of cryptic species have serious implications for accurate species identification, conservation management challenges, endangered species, invasive species, and cryptic diseases (Witt et al 2006; Bickford et al 2007; Nadler et al 2011; Pérez-Ponce & Poulin, 2016). Additionally, cryptic species can serve as agents for cryptic diseases, further emphasizing the importance of accurate identification for effective disease management and prevention. Yet, particularly in the case of small mammals, our understanding of the ecological distribution and taxonomic distribution of cryptic species remains limited, highlighting the need for further research and improved species identification methods.

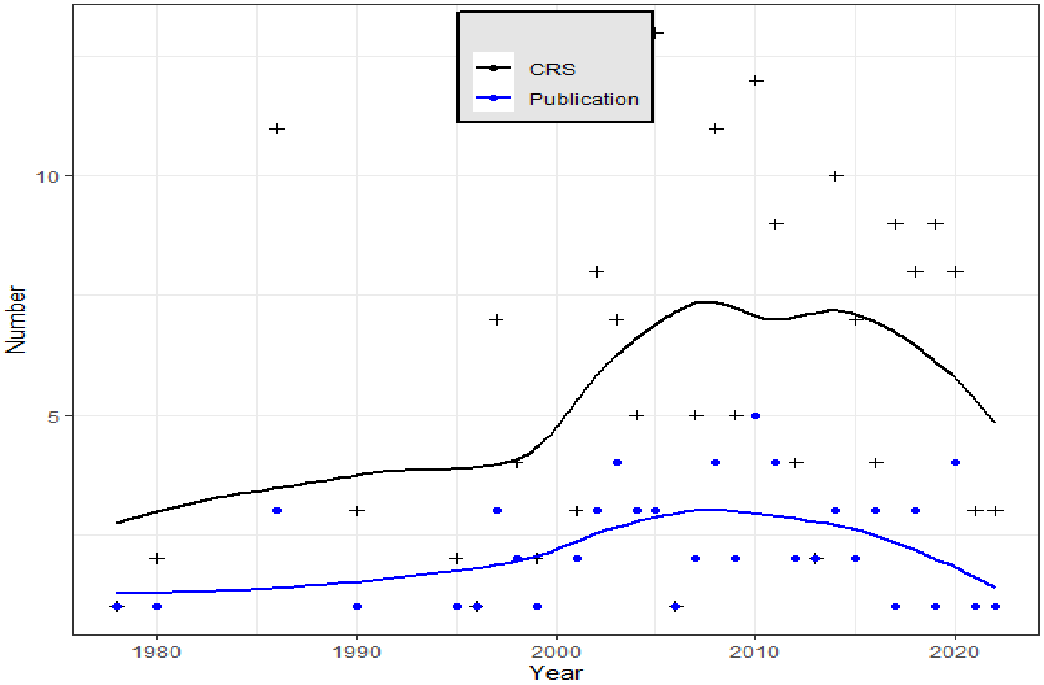

Figure 5. Scatterplot of the diversity of cryptic species reports per reviewed published studies

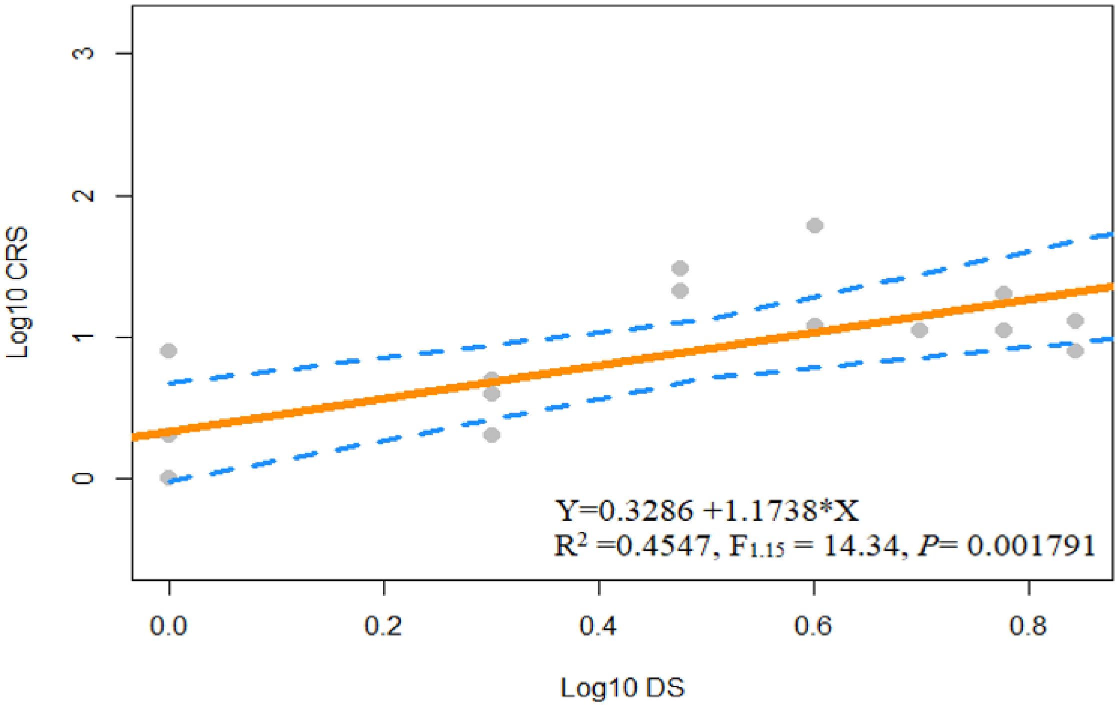

Figure 6. The log 10 of cryptic species (CRS) with log 10 number of described species across genera

The majority (34.78%) of our reviewed articles provide molecular data, while many of the articles (30.43%) use morphological methods of identification (morphometric measurements and cranial analysis). Karyotype (cytogenetic) and other techniques (spermatozoa, hemoglobin, ecological niche, and allozymic) account for 24.34% and 10.43% of the delineation techniques, respectively. Of the molecular data-based studies, 92.50% of the articles used cytochrome b mitochondrial DNA and 7.5% of them used nuclear. This confirms that molecular studies are better for defining cryptic genetically distinct groups. Most of the reviewed articles (33.91%) applied two or more identification methods to detect cryptic species (Fig. 5). Integrative identification methods are the foundation of cryptic species taxonomic delineation and description, as well as contribute to conservation efforts (Jörger & Schrödl, 2013). Although untouched cryptic species have been discovered as a result of the use of novel methods and the increased number of researchers in the field, a large number of these species remain undiscovered, particularly in small mammals such as bats and rodents. Many cryptic bat and wood mouse rodent species, for example, have recently been reported using bioacoustics (Jacobs *et al*., 2006; Ancillotto *et al*., 2017).

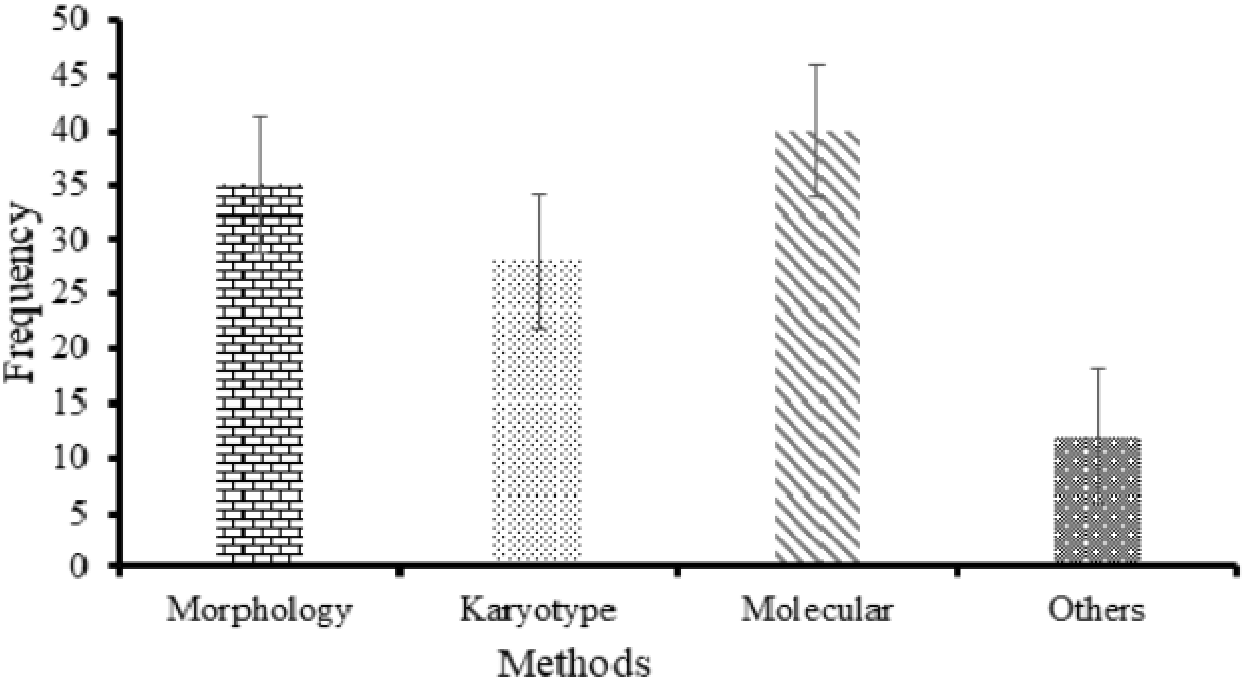

Figure 7. Methods that are used in the reviewed articles to delineations the described cryptic species

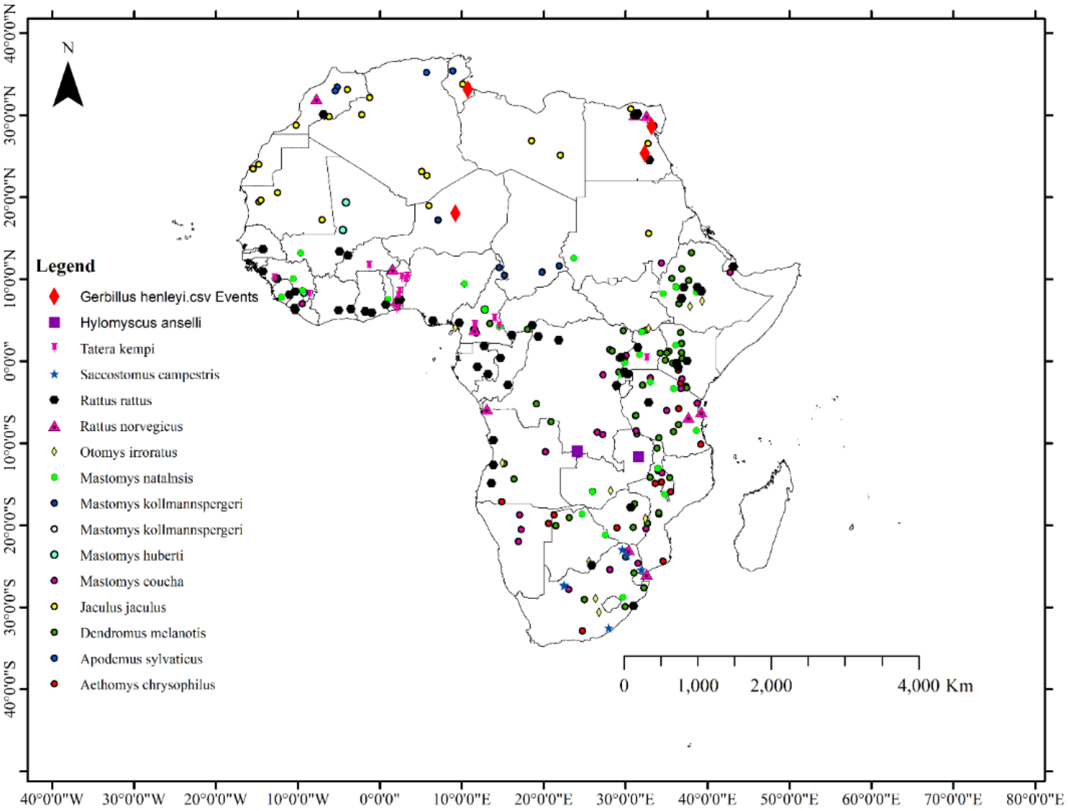

Figure 8. Distributions of representative cryptic species across a continent

We also reviewed more than 12 peer-reviewed articles, which confirm that species have diverse consequences for health such as reservoirs of zoonotic diseases (Rabiee *et al*., 2018) and estimation and conservation challenges (Struck *et al*., 2018). Since cryptic pests are challenging to identify and manage, better-quality pest supervision approaches and molecular and behavioral approaches may help (Mendelson and Shaw, 2002; Matsuda *et al*., 2013). Our review results also show that many rodent species are reservoirs for cryptic zoonotic diseases like Lassa fever in west Africa (Gibb *et al*., 2017). The existence of cryptic species is a biological issue in many aspects (Bickford *et al*., 2007; Korshunova *et al*., 2019). The majority of rodent species, especially cryptic, are host to more than 60 zoonotic diseases, and they are typical of fears for health (Pagès *et al*., 2010). The cryptic species has notably consequences in agriculture as crop pest and human health issues as parasites, pathogen vectors, or biological control agents (Matsuda *et al*. 2013; Navia *et al*., 2013; Walter and Proctor, 2013; Skoracka *et al*., 2015).

Table 1. Several methods important to delimit cryptic lineages, as well as their descriptions and authors

Methods to delimited cryptic species	Description	Authors
Morphological (morphometric) analysis	Although morphometric and physiological techniques are useful for identification, they do not ensure accurate identification of species lineages, particularly cryptic or sibling) species.	(Roldan *et al*., 1985; Hoskin *et al*., 2005; Saez and Lozano, 2005; Nadler and De Len, 2011; Jorger and Schrodl, 2013; Eme *et al*., 2018; Rossi *et al*., 2018)
Molecular analysis	Multiple approaches and marker have been widely used and more effective, low cost and rapid to delineate morphologically cryptic species and discovering new species possibility. It overcoming the taxonomic challenges. For example, four Muridae cryptic species were identified	(Lecompte *et al*., 2005⁝ Bickford *et al*., 2007; Pfenninger and Schwenk, 2007; Rueness *et al*., 2011; Jorger and Schrodl, 2013; Cardenosa *et al*., 2014; Nantarat *et al*., 2014; Egea *et al*., 2016; Eme *et al*., 2018; Fiser *et al*., 2018; Saleh *et al*., 2018; Chenuil *et al*., 2019; Moutinho *et al*., 2020)
Cytogenetic (Karyotype)	Comparative cytogenetics methods are very important for detecting cryptic and novel biodiversity in species and clear understanding nature and position important for taxonomic identification including cryptic rodents.	(Robinson, 2001)
Spermatozoa	Important to identify more related species, but cannot use for fossil. Spermatozoa are varying along rodent species	(Roldan *et al*., 1985;1992; Baker and Bradley, 2006; Burgin *et al*., 2018; Rossi *et al*., 2018)
Ecological niche	The ecological niche model verifies the linage of species, although putative species might be paraphyletic or allopatric, which makes it difficult to apply to all taxa, such as most cryptic species are sympatric but may not interbreed. It identified unique genetic lineages with similar ranges, supporting *Jaculus jaculus* and *J. hirtipes*'	(Hebert *et al*., 2004; Smith *et al*., 2005; Stuart *et al*., 2006; Adams *et al*., 2014; Moutinho *et al*., 2020)
Reproductive isolation	Interbreeding between animals is important to describe on the principles of monophyly with reproductive barriers, but there is difficulty in identifying reproductively isolated species.	(Mayr, 1942; Dobzhansky, 1950; 1971; Baum, 2016).
Track footprints	It is better for identifications of morphologically indistinguishable animals, including invasive rats and cryptic species. Accurate estimate and compositional diversity depend on it as well.	(Russell *et al*., 2009; Kozhevnikova *et al*., 2021)
Integrative analysis techniques	Genetic and a variety of morphometric methods are better for *cryptic* species or taxa group identification, like *Otomys*, *Lophuromys*, *Desmomys yaldeni*, *Aethomys kaiseri*, and *Microdillu speeli.*	(Bryja *et al*., 2019)
Bioacoustics analysis	Identify behavioral ecology and practical monitoring using animal calls (vocalization). Can distinguish two or mor morphologically similar species. Other evidences: Birds (Clemins and Johnson, 2002), Elephants (Clemins and Johnson 2002), bats (Vaughan and Harris 1997; Parsons and Jones, 2000; Parsons, 2001), shrew (Zsebo'k *et al*., 2015), Africa lions (Trapanotto *et al*., 2022), wood mice (Ancillotto *et al*., 2017), wolves (Larsen *et al*., 2022).	(Zsebo'k *et al*., 2015; Stowell *et al*., 2019)

Conclusion and conservation implications

In a time of biodiversity crisis, this is a golden age for the rapid and efficient discovery of cryptic and new species due to the molecular methods to delineate them in developing countries. However, there are still many taxonomic issues that need to be answered, and the understanding of species concepts is still lacking. Furthermore, in the practical environment, no precise conclusion on the existence of cryptic, speciation, and continuous evolutionary process was ever reached. The majority of the reviewed literature indicates that the use of various integrative methods is more effective in delineating cryptic taxa groups than depending on limited techniques. Morphological taxonomies alone, which may potentially lead to misleading guides to phylogenetic relationships in the wide range of species and taxa that remain controversial, particularly for cryptic species. Recently, cryptic species have become a significant component of biodiversity, but many of them are still untouched as such, particularly small mammals and developing countries. In order to accurately reflect cryptic diversity in an ecological context, a comprehensive reevaluation of biodiversity distinct species employing multivariate approaches is promoted. The existence of cryptic taxa may cause impairment in our estimation of biodiversity, species conservation management, disease control (including pandemic diseases), and control of invasive species. Contrarily, implementing the strategies experts suggested and understanding cryptic provides conservation with a stronger foundation and enables us to handle a range of outstanding ecological issues, including speciation, mutation, evolution, stasis, convergence, divergence, and understand conservation biology.

On the other hand, reliable assessments of the component's biodiversity are crucial for comprehending its effects in a variety of biological fields. The discovery and understanding of cryptic rodent species from the heterogenous biodiversity have significant values for improve conservation strategies in the ecological and species level. Integrative and danced species delineation techniques are critical for understanding many ecological questions and biological implications, such as evolutionary parallelism, independent evolution of taxa, ancestral character, consequences for speciation, and ecological roles.

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