TAXONOMIC IDENTIFICATION USING VIRTUAL PALAEOONTOLOGY AND GEOMETRIC MORPHOMETRICS: A CASE STUDY OF JURASSIC NERINEOIDEAN GASTROPODS

by YAEL LESHNO AFRIAT¹,², YAEL EDELMAN-FURSTENBERG², RIVKA RABINOVICH¹, JONATHAN A. TODD³ and HILA MAY⁴,⁵

¹The Fredy & Nadine Herrmann Institute of Earth Sciences, The National Natural History Collections of The Hebrew University of Jerusalem, Edmond J. Safra Campus, Jerusalem 9190401, Israel; yael.leshno@mail.huji.ac.il
²Geological Survey of Israel, 32 Yeshayahu Leibowitz Str., Jerusalem 9692100, Israel
³Department of Earth Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UK
⁴Department of Anatomy & Anthropology, Sackler Faculty of Medicine, Tel Aviv University, Tel Aviv 69978, Israel
⁵The Dan David Center for Human Evolution & Biohistory Research, Sackler Faculty of Medicine, Tel Aviv University, Tel Aviv 69978, Israel

Abstract: Taxonomic identification of fossils is fundamental to a wide range of geological and biological disciplines. Many fossil groups are identified based on expert judgement, which requires extensive experience and is not always available for the specific taxonomic group at hand. Nerineoideans, a group of extinct gastropods that formed a major component of Mesozoic shallow marine environments, have distinctive internal spiral folds that form the basis for their classification at the genus level. However, their identification is often inconsistent because it is based on a set of selected characters reliant upon individual interpretation. This study shows a non-destructive and quantitative method for their identification using micro-CT and geometric morphometrics. We examined and micro-CT-scanned nerineoidean specimens from five main families that dominated Europe, Arabia and Africa during the Middle–Late Jurassic. Optimal longitudinal slices were selected from the tomographic reconstructions or from images of polished cross-sections compiled from fossil collections, published work and online databases. Internal whorl outlines were represented by 30 evenly distributed sliding semilandmarks and shape variations were studied using the Procrustes-based geometric morphometrics method. Multivariate analysis shows that Ceritellidae and Ptygmatididae are distinct families, whereas Nerinellidae, Eunerineidae and Nerineidae fall within the same shape variance and cannot be distinguished based on internal whorl outlines. The suggested method can be applied to images from various sources as well as to poorly preserved specimens. Our case study demonstrates the importance of quantitatively re-evaluating taxonomy in the fossil record, promoting the future utility of large datasets.

Key words: virtual palaeontology, geometric morphometrics, Nerineoidea, Mesozoic, Jurassic, micro-CT.

The accurate identification of fossils lies at the heart of palaeontological biodiversity exploration and forms the foundation of systematic taxonomy, biostratigraphy, palaeoecology, evolutionary research and global change studies among other disciplines. By necessity, fossil specimens are identified based on their morphology and accurate and precise identification requires extensive expertise in the specific taxonomic group at hand. With the classical approach to morphological identification, taxa are frequently identified based on a set of selected characters that not infrequently remain inadequately described and documented. Therefore, their value in identification is dependent on individual interpretation. In addition, many taxa were described long ago and have remained poorly described and delimited; therefore identifications may be difficult to verify, resulting in possible misinterpretations and inaccuracies (MacLeod et al. 2010). These discrepancies have become increasingly apparent in recent years, following the rise in palaeontological ‘Big Data’ studies (Allmon et al. 2018). The digital availability of morphological information is rapidly increasing through the digitization of specimens held in museum collections, literature (e.g. Biodiversity Heritage Library), and researcher’s morphological data sets (increasingly...
including 3D and micro-CT imaging). However, the research value of such morphological data is dependent upon the accuracy of its metadata, including taxonomic identifications. Our growing ability to combine data from many sources has highlighted the great importance of ensuring taxonomic accuracy and consistency. Both specimen-based (e.g. Global Biodiversity Information Facility) and literature-based taxonomic databases (e.g. Paleobiology Database) are faced with a growing need to re-evaluate the consistency of the taxonomic identifications they serve, to ensure their research value into the future (Karim et al. 2016; Nelson & Ellis 2018). Thus, finding new ways to analyse complex shapes in order to recognize the underlying taxonomic signal will help practical identification of fossil taxa and should facilitate and strengthen the many palaeontological studies that are reliant upon uniform identifications (Carvalho et al. 2007; Ramírez et al. 2007; Faulwetter et al. 2013). In addition, it is likely to reveal new insights into the morphology and hence taxonomy and classification of those taxa that remain contentious.

A notable example of the need to re-evaluate the robustness of taxonomy and systematics in the fossil record is exhibited by the extinct gastropod superfamily Nerineoidea Zittel, 1873. Gastropods are a dominant component of sedimentary rocks and have a rich and extensive fossil record (Kidwell & Bosence 1991, Bieler 1992). An example of the practical importance of consistent and accurate taxonomic identification of fossil gastropods is emphasized by their use as sensitive indicators of seaﬂoor properties and a useful tool for palaeoenvironmental reconstruction (Kidwell & Flessa 1995; Dietl et al. 2015). Presence of common Nerineoidea characterized many shallow shelf carbonate environments from the Early Jurassic (Hettangian) to the Late Cretaceous (Maastrichtian) (Dietrich 1925; Cox 1949) across Europe, Africa, Asia and North and South America (Cox 1965; Pchelintsev 1965; Wieczorek 1979; Sohl 1987; Vaughan 1988; Sirna 1995). These large and conspicuous gastropods are considered to be key faunal elements of Mesozoic carbonate ramps and platforms and were especially common in the tropical Tethys Sea (Sohl 1987; Kollmann 1992). As one of the most abundant macrofossil components of many Mesozoic shallow marine environments, nerineoideans have been extensively used for biostratigraphy and palaeoecology (Cox 1965; Wieczorek 1979, 1998; Sirna & Mastroianni 1993; Barker 1994). Their palaeoecological and biostratigraphical importance is reflected in their abundant occurrence in fossil collections and their numerous citations in the scientific literature (Vaughan 1988; Kollmann 2014).

The expansion of carbonate platforms in the Middle Jurassic promoted nerineoidean diversification and led to them being among the most common and distinctive gastropods found in Jurassic strata worldwide (Sohl 1987; Barker 1990, 1994; Wieczorek 1998). They are known to form mass accumulations that can reach a density of hundreds of specimens per square metre. These nerineoidean-rich fossil beds can extend laterally for kilometres and may be useful stratigraphic marker beds (e.g. Reuchenette Formation, Switzerland) (Wieczorek 1979; Waite et al. 2008). Nevertheless, the group’s taxonomy is challenging and its systematic description and phylogenetic position debated (Tracey et al. 1993; Sirna 1995).

Nerineoideans are notable for possessing prominent internal spiral lamellae (folds) that extend from the internal walls of the shell into the shell cavity (Fig. 1A) (Cossmann 1898; Cox 1960; Bandel 1993; Barker 1994). Nerineoidean taxa show a very wide diversity in the number, morphology and strength of their folds. The folds vary in occurrence across taxa from those with no, or very few, folds to those with five extremely convoluted folds with many lobes (e.g. Kouyoumontzakis 1989, fig. 3, pl. 1). The number and position of folds may change markedly through the ontogeny of an individual, however it remains fairly constant within a species across comparable stages of growth (e.g. Wieczorek 1979, Barker 1990). These features have made their description essential in species identification and they are a cornerstone for the taxonomy and classification of the superfamily (Sirna 1995). Each whorl interior may be characterized by the presence of folds in four positions as seen in whorl cross-sections: on the columella, parietal, pallial and basal walls (Fig. 1B; Cox 1960; Vaughan 1988). The positional identification of folds has provided the basis for a simple descriptive notation or ‘fold formula’ (Barker 1990). This has been extended by others (e.g. Wieczorek 1979) into a complex notational system describing up to three orders of folds in the most complexly folded taxa together with more minor swellings or flexures. It should be stressed that, to our knowledge, these descriptive systems have not been explicitly regarded as reflecting biological homology of fold structures among nerineoidean taxa.

Folds are incrementally secreted over the internal walls of the shell during ontogenetic development and can reduce the internal volume of the shell by 50%, but the shell remains fold-free in the very earliest whorls and at least part of the last whorl (Barker 1990; Waite et al. 2008). Historically, a range of interpretations have been offered for the function of nerineoid folds and these are reviewed by Kollmann (2014).

Numerous researchers have contributed to nerineoidean classification (Defrance 1852; Cossmann 1898; Cox 1960; Pchelintsev 1965) and systematic revisions (Delpey 1940; Wieczorek 1975; Vaughan 1988; Barker 1990; Bandel 1994; Sirna 1995). Early classifications considered the Nerineoidea as belonging to the
Prosobranchia (Cossmann 1896; Wenz 1940), while in a major later revision they were placed with the superfamily Murchisonoidea in the order Muchisoniata (Pchelintsev 1965), and were regarded as polyphyletic. Following work by Vaughan (1988) and Bandel (1994), Nerineoidea are today recognized as a clade lying within the subclass Heterobranchia, as indicated by their shared presence of a heterostrophic protoconch (Kollmann 2014). Very useful historical summaries of changing nerineoidean classifications across a range of taxonomic levels have been provided by Kouyoumontzakis (1989) and Sirna (1995).

The most recent revision by Kollmann (2014) redefined the superfamily Nerineoidea, and recognized seven families using a set of morphological criteria in which the relative importance of different character complexes was stressed at different hierarchical levels within the classification. For example, at family level taxonomic assignment was based predominantly on the shape of the base of the last whorl and the siphonal apparatus (Kollmann 2014), even though these features are rarely preserved. At the generic level, Kollmann (2014) identified and classified taxa based on the interpretation of internal folds within the whorls and the external whorl outline, both of which are commonly preserved. Kollmann (2014, p. 352) noted that for higher level classification, ‘generally, variations in the shape and size of internal plaits [herein folds], which frequently have been used to distinguish species, are not suitable criteria. Changes with ontogeny, variability and even different cutting planes or differences in preservation obscure actual plait size and shape.’ Despite what Kollmann affirmed, he reported some characters of internal folds in his diagnoses of the families. Kollmann’s (2014) classification should be regarded primarily as a practical (= artificial) system; clearly a phylogenetic classification of the Nerineoidea still remains some way distant.

The internal morphology of the whorls is classically observed in polished cross-sections of specimens, and these often complex morphologies are generally described in detail. Nonetheless, the inconsistency between different researchers on taxonomic importance at different hierarchical levels of these descriptions has helped create taxonomic controversy (Sirna 1995). In spite of these limitations, the morphology of the internal whorl cross-sections still remains the foundation for establishing the generic position of nerineoidean species (Waite et al. 2008; Kollmann 2014).

Virtual palaeontological methods combined with shape analysis using geometric morphometric (GM) methods are increasingly contributing to our understanding of taxonomy, evolution and phylogeny across a wide range of organisms (Sutton 2008; Adams & Otárola-Castillo 2013) and have helped promote the notion of automated taxonomic identification (MacLeod 2007). Virtual palaeontology uses three-dimensional (3D) reconstructions of fossils

![FIG. 1. Nerineoidean fold morphology and terminology in: A, cross-section of Ptygmatis nodosa? (Callovian, Israel; GSI 7150); B, schematic illustration of one internal whorl outline of Eunerinea sp. showing four simple folds (modified after Hirsch 1980; and Barker 1990). Scale bar represents 1 cm.](image-url)
from computerized tomography (CT) scans to study morphology across a wide range of preservation states and specimen sizes (e.g. Tafforeau et al. 2006; Cunningham et al. 2014; Rahman & Smith 2014; Gueriau et al. 2018). The use of tomographic methods, such as micro-CT scans, can reveal complex internal structures of fossilized organisms that have been inaccessible so far (Molineux et al. 2007; Sutton 2008; Faulwetter et al. 2013). This has enabled researchers to analyse structures using GM methods such as landmarks and semilandmarks without causing any damage to the specimen (MacLeod 2007; Sutton et al. 2014, 2016). Thus, the distinctive internal structure of nerineoideans is ideally suited for developing a quantitative approach based on virtual palaeontology and GM methods. Moreover, a tomographic and quantitative approach to characterizing these features may provide a uniform measure that can help understand systematic relationships of nerineoidean taxa and how those are best represented in a taxonomic classification (e.g. Delpey 1940; Vaughan 1988; Sirna 1995; Kollmann 2014). In the current study, we initiate the development of a new reliable quantitative taxonomic identification method for nerineoideans using semilandmark-based GM.

**MATERIAL AND METHOD**

A total of 58 specimens were examined from a wide range of Middle and Upper Jurassic palaeolatitudes, including localities from Europe, Asia (Arabia) and Africa in order to capture a wide range of cross-sectional shell morphologies from across the Tethys shelf (Fig. 2). The ecologically most abundant five of the seven known nerineoidean families (sensus Kollmann 2014) in the Tethys Sea were included in the analysis: Ceritellidae Wenz, 1940; Ptygmatidae Pchelintsev, 1960; Nerinellidae Pchelintsev, 1960; Eunerineidae Kollmann, 2014; and Nerineidae Zittel, 1873. Synonyms of species and genera were updated to establish a taxonomic baseline for further analysis. An updated systematic classification was based on Kollmann (2014) as used by Bouchet et al. (2017), the latest classification of fossil and living gastropods. Heinz Kollmann revised species names and systematic position for some of the specimens (H. Kollmann, pers. comm. 2018).

Of the specimens, 28 were scanned at the Natural History Museum (London, UK) using a micro-CT (X-Tek HMX ST225 cone beam system, Nikon Metrology; voltage of 180–200 kV, current/flux of 180–200 μA; 3142 projections were collected at 0.11° angular intervals/slice increment over a 360° rotation with a voxel size of 0.018 to 0.09 mm). The rest were analysed using images of polished cross-sections compiled from various sources (Table 1; Leshno Afriat et al. 2020, appendix S1).

**Institutional abbreviations.** GSI, Geological Survey of Israel; NHMUK, Natural History Museum, London, UK.

**Capturing internal whorl shape**

**Internal whorl shape from micro-CT scans.** The workflow for shape capturing of the internal whorl outline from CT images is illustrated in Figure 3A–D. Specimens that were suspected of having density differences between the shell and the whorl interiors were targeted for CT-scanning. Three-dimensional digital models of nerineoideans were built using the Amira 6.4 software package (Mercury Computer Systems, Chelmsford, MA). In addition to 13 individually scanned specimens, nerineoidean specimens were manually segmented from a mass accumulation sample from the Upper Jurassic of Tanzania (NHMUK PI G 46024; Leshno Afriat et al. 2020, appendix S1; Fig. 4). An optimal 2D slice showing the internal whorl outlines was selected for each individual 3D model using Amira 6.4 (Figs 3C, 4C). To capture ontogenetic variance in internal whorl outline, three successive longitudinal whorl cross-sections showing the internal folds were analysed for each specimen. Whorls were captured from the central part of the spire where the internal fold structure was most visible and complex. The apex and adapical part of the penultimate whorl, which generally remain fold-free (Barker 1990; Waite et al. 2008), were avoided. In cases where consecutive internal whorl outlines were unclear or incomplete, any available whorls were captured, with a maximum of six whorls per specimen. Thirty evenly spaced sliding semilandmarks were placed on the internal shape outline of each whorl, using Rhinoceros 3D v.1.5 (Robert McNeel & Associates, Seattle, USA). The sliding semilandmarks were distributed clockwise from a geometrically equivalent anchor point positioned at the most abaxial point in the curve between the pallial and basal folds (see Fig. 3D, F). The whorl cross-sections were numbered according to their respective location in the gastropod spire (W1 to W6; Fig. 3C, E). The outlines of internal whorls W4, W5, and W6 were mirrored prior to landmark spacing. A shifting semilandmark GM method (Zelditch et al. 2004; Bardua et al. 2019) employing a single anchor (start) point was used to prevent unwarranted assumptions concerning the homology of individual folds, as would be required using a landmark-based method. This outline method maximized the geometric correspondence across the semilandmark set.

**Internal whorl shape from polished cross-sections.** Images of polished cross-sections were obtained from published plates and online images from the Global Biodiversity Information Facility (GBIF 2019; see Leshno Afriat et al. 2020, appendix S1, for a list of specimen’s sources). In
addition, specimens from the palaeontological collections of the Geological Survey of Israel and the Natural History Museum, London (UK) were photographed (using X-T10 Fujifilm, and a Canon EOS 600D, respectively) and their internal whorl shape captured in an identical way (Fig. 3E, F).

**Data analysis**

Statistical analyses were conducted in R (version 3.6.1) using the package geomorph (v. 3.1.3) (Adams & Otárola-Castillo 2013) and PAST v. 3.19 (Hammer et al. 2001). Shape coordinate data were transformed using General Procrustes Analysis to standardize information about position, orientation and size (Zelditch et al. 2004). Analysis of similarity (ANOSIM) was used to test for morphological variation in internal whorl shape through ontogeny between and within specimens of each of the studied families. Intra- and inter-observer variations of the method were examined on five specimens by two independent researchers. Each of the researchers identified an optimal CT-slice, and then one of the researchers (YLA) repeated the distribution of landmarks from the equivalent starting point three times. Principle component analysis (PCA) and ANOSIM were carried out to examine the repeatability of the results (Leshno Afriat et al. 2020, appendix S2). The validity of our method of combining cross-sections from CT-slices and images of polished specimens was established using two specimens of *Eunerinea*? sp. (GSI 3161, GSI 3162; Leshno Afriat et al. 2020, appendix S1) that were CT-scanned, polished and their cross-sections photographed. PCA showed our method to be highly reliable and repeatable (Leshno Afriat et al. 2020, appendix S2).

Canonical variates analysis (CVA) was performed for corrected estimation rates of assignment of specimens to family level. Permutational multivariate analysis of variance (PERMANOVA) was carried out on the entire shape space to examine significant differences between a priori groups. PCA was used to examine the shape variance of internal whorl outlines in different genera for each of the five studied families.

**TABLE 1.** The number of specimens analysed for each of the five nerineoidean families using either CT images or polished cross-sections.

| Family        | Images of polished cross-sections | Cross-sections sliced from micro-CT scans | Total |
|---------------|------------------------------------|------------------------------------------|-------|
| Ceritellidae  | 4                                  | 3                                       | 7     |
| Ptygmatididae | 9                                  | 9                                       | 9     |
| Nerinellidae  | 11                                 | 23                                      | 34    |
| Eunerineidae  | 1                                  | 2                                       | 3     |
| Nerineidae    | 5                                  | 28                                      | 5     |
| Total         | 30                                 | 28                                      | 58    |
RESULTS

Internal whorl outline significantly differentiates three groups of nerineoideans, two comprising single families, independent of data source (Table 1; Fig. 5). No significant difference is found between consecutive internal whorls of ontogenetic development, represented by the relative position of the whorl in the gastropod spire (W1, W2, W3 etc.) \((R = -0.06, p = 0.92)\). Ceritellidae and Ptygmatididae are significantly separated from each other and from the other groups, whereas the variance of the sampled specimens belonging to the families Nerinellidae, Eunerineidae and Nerineidae strongly overlaps (Fig. 5, Table 2). Accordingly, we combined the specimens belonging to Nerinellidae, Eunerineidae and Nerineidae into one group for further analysis. CVA demonstrates moderate to high correct estimation rates for each group (i.e. Ceritellidae, Ptygmatididae and Nerinellidae + Eunerineidae + Nerineidae) ranging from 75.0% to 90.4% (Table 3). Variance in internal whorl shape separates

FIG. 4. Workflow for shape extraction from a complex fossil bed: A, planar and lateral view of a mass accumulation of Nerineoidea from the Kimmeridgian (Upper Jurassic) of Tanzania (NHMUK PI G 46024); B, 3D model in planar and lateral view of manually segmented fossil specimens (carbonate matrix in grey, segmented specimens in colour); C, enlarged single specimen in blue. For each segmented specimen an optimal 2D slice is selected and longitudinal internal whorl cross-sections are extracted as illustrated in Figure 3C. Scale bars represent 1 cm.
species of the same family along the first two PC axes for Ceritellidae and Ptygmatididae (Fig. 6A, B). For example, in the Ceritellidae (Fig. 6A), internal whorl outlines of *Fibuloptyxis bucillyensis* Fischer, 1960 and *Fibuloptyxis elegans convexa* Fischer, 1960 plot more closely to each other than to specimens of *Cossmannia*, regardless of the number of studied internal whorl outlines, the relative position in the spire and the different methods of obtaining cross-sections (Table 1).

The first two PCs explain 88% of the total shape variance for the Ceritellidae (Fig. 6A), which are generally characterized by having a simple outline with strong palial or parietal folds (Kollmann 2014). The number of folds increases along PC1 (75%), while the columellar fold becomes more pronounced along PC2 (13%) (Fig. 6A). In the Ptygmatididae, which are defined by highly convoluted whorls with two columellar folds and complex parietal and pallial folds (Kollmann 2014), the first two PCs explain 61% of the total shape variance (Fig. 6B). Internal whorl shape becomes more complex along PC1 (44%) and with more lobes along PC2 (17%).

In the PCA of the combined Nerinellidae + Eunerineidae + Nerineidae group, the first two PC axes explain 67% of total variance. The high resemblance in fold morphology prevents discrimination between whorls of sampled specimens belonging to these three families: the characteristics of the inner whorl outlines are indistinguishable. These families show varying degrees of development of the columellar folds and more prominent pallial and parietal folds (Fig. 6C).

**DISCUSSION**

This study demonstrates a reliable and quantitative method of investigation of the internal morphological features of spire whorls that can be applied to the dominant nerineoidean families of the Tethys Sea during the Middle and Late Jurassic. Quantitative shape analysis significantly differentiates between specimens of the Ceritellidae, Ptygmatididae and Nerinellidae + Eunerineidae + Nerineidae families, based on their internal whorl outlines (Fig. 5; Tables 2, 3). Within our dataset, this separation extends to species level of the Ceritellidae and Ptygmatididae families (Fig. 6A, B). Furthermore, our method is independent of sample size and applicable to different data sources (Tables 1, 2).

Additionally, our method suggests that there may be no clear geometrical difference in interior whorl morphology between the sampled specimens of Nerinellidae, Eunerineidae and Nerineidae (Figs 5, 6; Table 2) that is usable for their taxonomic differentiation. These families are known for their complicated systematic history, which has been the focus of strong debate (Vaughan 1988; Sirna 1995). Zittel (1873) established the family Nerineidae based on the possession of a posterior sinus and slit band. Cossmann (1896) was the first to assign the genera *Nerinea* and *Nerinella* to the family Nerineidae based on the occurrence of a sutural band and the position and orientation of the slit and aperture. Following Cossmann (1896), numerous researchers either grouped or separated the genera *Nerinea* and *Nerinella* across different

![FIG. 5. Canonical variates analysis (CVA) of variation in internal whorl outlines for the five studied Nerineoidea families.](image-url)
hierarchical levels based on various features, such as overall shell shape, the presence of a heterostrophic protoconch, ornamentation and the presence or absence of an umbilicus (summarized in Vaughan 1988). In a later revision by Pchelintsev (1965), which massively inflated the number of higher level nerineoid taxa, these genera were elevated to the family level (viz Nerineidae and Nerinellidae) based on the presence of an anterior siphonal notch and general shell shape. The genus *Eunerinea* was first proposed by Cox (1949) as a subgenus for forms previously attributed to *Nerinea* by Cossmann (1896). A more recent revision by Kollmann (2014) redefined the Nerinoidea (n. fam.) that includes the Nerineidae Zittel, 1873 *sensu* Pchelintsev (1965) and also the Diptyxidae Bouchet & Rocroi, 2005, which was based on the mistaken relationships of *Diptyxis* (now shown to belong to the Ceritellidae).

Whereas internal whorl outline is widely agreed as the basis for classification and identification of nerinoidean taxa at species level (e.g. Vaughan 1988; Sirna 1995; Kollmann 2014), classification at higher taxonomic levels has been established using various external shell features. This has resulted in the establishment of a wide range of classifications across different taxonomic levels among different authors (see summary in Sirna 1995). Our method demonstrates, in a quantitative way, that it is not possible using our sampled specimens to differentiate the families Nerinellidae, Eunerineidae and Nerinidae based on their internal structure alone (Figs 5, 6C). Kollmann’s familial diagnoses suggest a potential similarity of internal whorl morphology amongst members of these families; most of the diagnostic differences between them relate to external morphological features and size. Thus, the systematic position and further subdivision of genera from these families remains problematic, and further examination is needed to validate their taxonomic assignment. We envisage that future refinement of the classification of the Nerinoidea will be best accomplished by combining the information obtained from ontogenetic and GM studies of interior whorl morphologies with the external morphological characters currently used. In this way we can obviate the inherent artificiality of a classification built using different characters at different hierarchical levels.

Micro-CT has been used to help in reconstructing the anatomy of recent and fossil molluscs, including buccal masses of ammonoids (e.g. Tanabe *et al.* 2013; Kruta *et al.* 2014) and extant cephalopods (e.g. Kerbl *et al.* 2013). Previous tomographic reconstructions of the internal structure of mollusc shells have focused on 3D parameters, such as chamber volume, to test buoyancy properties (Lemanis *et al.* 2015) and to study evolution and development (Tajika *et al.* 2015, 2018; Lemanis *et al.* 2016). However, imaging of fossils has been limited to relatively few specimens (e.g. Lemanis *et al.* 2015, 2016; Tajika *et al.* 2015) and scanning was restricted to just those exceptionally preserved fossils that exhibited a clear contrast between the shell and the surrounding matrix. We also found micro-CT scanning useful in reconstructing the internal structure of fossils without damaging them through physical preparation. However, our method of using slices of cross-sections from the scanned 3D models made it possible to analyse specimens with various degrees of preservation, specifically poorly preserved ones. Furthermore, by incorporating the large amount of available cross-section images from fossil collections, publications and online databases we significantly increased our sample size.

### Table 2. PERMANOVA Bonferroni significance p-values for pairwise comparisons of the five studied Nerinoidea families.

| Family         | Nerinellidae | Nerineidae | Ceritellidae | Ptygmatididae | Eunerineidae |
|----------------|--------------|------------|--------------|---------------|--------------|
| Nerinellidae   | 0.94         | 0.001      | 0.001        | 0.141         |              |
| Nerineidae     | 0.94         | 1          | 0.009        | 1             |              |
| Ceritellidae   | 0.001        | 1          | 0.001        | 0.011         |              |
| Ptygmatididae  | 0.001        | 0.009      | 0.001        | 0.001         |              |
| Eunerineidae   | 0.141        | 0.011      | 0.001        |               |              |

Numbers in **bold** indicate a significant difference between groups (p < 0.05).

### Table 3. Correct estimation rates for Ceritellidae, Ptygmatididae and the combined specimens of Nerinellidae + Eunerineidae + Nerineidae using canonical variates analysis (CVA) and Jackknife method.

| Group                        | Correct estimation rate (%) |
|------------------------------|-----------------------------|
| Ceritellidae                 | 82.6                        |
| Ptygmatididae                | 75.0                        |
| Nerinellidae + Eunerineida + Nerineidae | 90.4               |
| Total                        | 87.3                        |

Micro-CT has been used to help in reconstructing the anatomy of recent and fossil molluscs, including buccal masses of ammonoids (e.g. Tanabe *et al.* 2013; Kruta *et al.* 2014) and extant cephalopods (e.g. Kerbl *et al.* 2013). Previous tomographic reconstructions of the internal structure of mollusc shells have focused on 3D parameters, such as chamber volume, to test buoyancy properties (Lemanis *et al.* 2015) and to study evolution and development (Tajika *et al.* 2015, 2018; Lemanis *et al.* 2016). However, imaging of fossils has been limited to relatively few specimens (e.g. Lemanis *et al.* 2015, 2016; Tajika *et al.* 2015) and scanning was restricted to just those exceptionally preserved fossils that exhibited a clear contrast between the shell and the surrounding matrix. We also found micro-CT scanning useful in reconstructing the internal structure of fossils without damaging them through physical preparation. However, our method of using slices of cross-sections from the scanned 3D models made it possible to analyse specimens with various degrees of preservation, specifically poorly preserved ones. Furthermore, by incorporating the large amount of available cross-section images from fossil collections, publications and online databases we significantly increased our sample size.
We demonstrate, for the first time to our knowledge, that micro-CT scanning is also useful for establishing the internal morphology of specimens embedded in complex calcareous mass-accumulation beds (Fig. 4) (but see Lukeneder et al. (2014) for laser scanning of surface morphology). Mass accumulations of shells, or fossil concentrations, have been extensively studied for their usefulness in sedimentology and stratigraphy as well as for the wealth of palaeobiological data they hold (Kidwell et al. 1986). The taphonomic analysis of fossil concentrations has been correlated with multiple palaeoenvironmental parameters, including palaeohydraulics and sedimentary deposition, facies analysis and marker bed correlations (Fürsich 1978; Kidwell et al. 1986) as well as sequence stratigraphy (Fürsich & Pandey 2003) and petrophysical properties (Chinelatto et al. 2020). Mass accumulations of nerineoideans are considered important recorders of water energy and nutrient availability, and quantitative analysis of their abundance is used for environmental reconstruction in many regions (Dauwalder & Remane 1979; Wieczorek 1979; Waite et al. 2008). CT enabled us to isolate individual specimens from the surrounding matrix without using destructive and irreproducible mechanical or chemical methods (summarized in Sutton 2008). By combining virtual palaeontology and GM, we manually segmented nerineoidean specimens without harming the original sample and accurately characterized the internal structure of the nerineoidean specimens. Our new approach proposes a new opportunity of quantitative examination of mass accumulations of nerineoideans. It has the potential to uncover underexploited data on the intraspecific variation of fossil concentrations and to increase their value in palaeoenvironmental reconstructions and biostratigraphy.

The efficiency of GM in distinguishing between species using a single data source has been frequently shown for both Recent and fossil gastropods (e.g. Guralnik & Kurpius 2001; Carvajal-Rodríguez et al. 2006; Monnet et al. 2009; Smith & Hendricks 2013; Abdelhady 2016; Jackson & Claybourn 2018). However, we have developed a GM protocol that can be applied to multiple data sources: CT images, polished cross-sections and mass accumulations, all analysed using the same methods to determine the internal structure of the shell in 2D. This allows easy comparison of data across disparate sources including whole shells, sectioned shells and the frequent illustrations of cross-sections in published work. We envisage that the use of this method will help to enable the re-evaluation of the taxonomy and classification of the Nerineoidea using an easily replicable method. Previous work by Jackson & Claybourn (2018) emphasized the importance of incorporating classic qualitative criteria to create

**FIG. 6.** Principal component analysis (PCA) of internal whorl outlines and characteristic outlines of taxa within Nerineoidean families: A, Ceritellidae; B, Ptygmatidae; C, Nerinellidae + Eunerineidae + Nerineidae.
a robust framework for taxonomic identification of Cambrian helcionelloid molluscs. They combined qualitative systematic descriptors with geometric morphometrics analysis to refine subtle intra- and interspecific variations in shape. Our quantitative method of investigation of the characters of fossil gastropods might be seen as a step towards the development of a large-scale automated taxonomic identification system (MacLeod 2007; Hsiang et al. 2018).

CONCLUSIONS

We suggest a new reliable quantitative method to taxonomically identify nerineoideans based on their internal shell structures. We show that using micro-CT scanning and GM can provide a powerful and easily employed tool for identifying nerineoidean gastropods, one of the most abundant, diverse and widespread gastropod superfamilies of the Mesozoic. Our method is non-destructive and thus reduces the inherent difficulty associated with the existing classical morphological identifications of Nerineoidea. Moreover, it is applicable to a range of poorly preserved specimens, cross-sections, and to mass accumulations of specimens in fossil beds.

The current study found that the Ceritellidae and Ptygmatidae families show distinctive internal whorl outlines, whereas the internal whorl outline of the Nerinellidae, Eunerineidae and Nerineidae families overlap, thus demonstrating the need for further taxonomic re-evaluation of the group. Our suggestion for applying virtual palaeontology techniques to the identification of nerineoidean fossils could promote the revolution of their classification and understanding of their phylogeny. In turn, the distinct identification of nerineoideans can be applied to improve the characterization of macrobenthic community structure of Mesozoic carbonate platforms. The era of digitization enables us to ask large-scale questions based on the sampled fossil record. Using our virtual palaeontology approach on the current curated databases, we can progress towards a unified interpretation of taxonomic data, promoting the use of large datasets in future work.

Acknowledgements. We thank H. Kollmann from Naturhistorisches Museum Wien and H.K. Mienis from the National Natural History Collections, The Hebrew University of Jerusalem, for their assistance in taxonomic identification of specimens; and A. Pokhojaev from the Department of Anatomy and Anthropology, Dan David Center for Human Evolution and Biohistory Research, Tel Aviv University, for help with tomographic reconstructions. We thank C. Sendino from the Natural History Museum, London (UK) for her assistance. We thank Geological Survey of Israel staff for help with field work in Israel. Israel Ministry of Science and Technology grant no. 0399589 and Ministry of Energy and Water Resources grant no. 214-17-001 are greatly appreciated for their funding. This research received support from the SYNTHESYS Project http://www.synthesys.info/ which is financed by European Community Research Infrastructure Action under the FP7 Integrating Activities Program. Thomas A. Neubauer and Stefano Monari are thanked for their reviews, which improved the manuscript.

DATA ARCHIVING STATEMENT

Data for this study (including specimen list, PCA analysis results and CT-scan data) are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.7m0fcpxs4

Editor. Michael Hautmann

REFERENCES

ABDELHADY, A. A. 2016. Phenotypic differentiation of the Red Sea gastropods in response to the environmental deterioration: geometric morphometric approach. Journal of African Earth Sciences, 115, 191–202.

ADAMS, D. C. and OTÁROLA-CASTILLO, E. 2013. geomorph: an R package for the collection and analysis of geometric morphometric shape data. Methods in Ecology & Evolution, 4, 393–399.

ALLMON, W. D., DIETL, G. P., HENDRICKS, J. R. and ROSS, R. M. 2018. Bridging the two fossil records: paleontology’s “big data” future resides in museum collections. In ROSENBERG, G. D. and CLARY, R. M. (eds). Museums at the forefront of the history and philosophy of geology: History made, history in the making. Geological Society of America Special Paper, 335.

BANDEL, K. 1993. Caenogastropoda during Mesozoic times. Scripta Geologica Special Issue, 2, 7–56.

——. 1994. Triassic Euthyneura (Gastropoda) from St. Cassian Formation (Italian Alps) with a discussion on the evolution of the Heterostropha. Freiberger Forschungshefte-Reihe C-Geowissenschaften, 452, 79–100.

BARDUA, C., FELICE, R. N., WATANABE, A., FABRE, A. C. and GOSWAMI, A. 2019. A practical guide to surface sliding semi-landmarks in morphometric analyses. Integrative Organismal Biology, 1, 1–34.

BARKER, M. J. 1990. The palaeobiology of nerineacean gastropods. Historical Biology, 3, 249–264.

——. 1994. The biostratigraphic potential of Nerineacean Gastropods – case studies from the Middle Jurassic of England and the Upper Jurassic of France. Geobios, 27, 93–101.

BIELER, R. 1992. Gastropod phylogeny and systematics. Annual Review of Ecology & Evolution, 23, 211–238.

BOUCHET, P. and ROCROI, J.-P. 2005. Classification and nomenclator of gastropod families. Malacologia, 47 (1–2), 1–397.

—— ——. 2018. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia, 61, 1–526.
CARVAJAL-RODRÍGUEZ, A., GUERRA-VARELA, J., ROLÁN, E. and ROLÁN-ÁLVAREZ, E. 2006. An example of the application of geometric morphometric tools to the morphological diagnosis of two sibling species in Nassarius (Mollusca, Prosobranchia). *Iberus*, 24, 81–88.

CARVALHO, M. R. DE, BOCKMANN, F. A., AMORIM, D. S., BRANDÃO, C. R. F., VIVO, M. DE, FIGUEIREDO, J. L. DE, BRITSKI, H. A., PINNA, M. C. C. DE, MENEZES, N. A., MARQUES, F. P. L., PAPAVERO, N., CANCELLO, E. M., CRISCI, J. V., McEACHERAN, J. D., SCHELLY, R. C., LUNDBERG, J. G., GILL, A. C., BRITZ, R., WHEELER, Q. D., STIASSNY, M. L. J., PARENTI, L. R., PAGE, L. M., WHEELER, W. C., FAIVOVICH, J., VARI, R. P., GRANDE, L., HUMPHRIES, C. J., DESALLE, R., EBACH, M. C. and NELSON, G. J. 2007. Taxonomic impediment or impediment to taxonomy? A commentary on systematics and the cybertaxonomic-autoadaption paradigm. *Evolutionary Biology*, 34, 140–143.

CHINELATTO, G. F., BELILA, A. M. P., BASSO, M., SOUZA, J. P. P. and VIDAL, A. C. 2020. A taphofacies interpretation of shell concentrations and their relationship with petrophysics: a case study of Barremian-Aptian coquinas in the Itapema Formation, Santos Basin-Brazil. *Marine & Petroleum Geology*, 116, 104317.

COSSMANN, M. 1896. *Essais de paléoncologie comparée*, 2, The Author & Comptoir Géologique, 179 pp.

— 1898. Contribution à la paléontologie française des terrains jurassiques (Gastropodes): Nérines. *Mémoires de la Société Géologique de France*, 19, 1–179.

COX, L. R. 1949. On the genotype of *Nerinea*; with a new subgeneric name *Eunereina*. *Journal of Molluscan Studies*, 27, 248–250.

— 1960. Gastropoda: General characteristics of Gastropoda. 84–169. In MOORE, R. C. and PITRAT, W. (eds). *Treatise on invertebrate paleontology. Part I. Mollusca 1*. Geological Society of America & University of Kansas Press.

— 1965. Jurassic Bivalvia and Gastropoda from Tanganyika and Kenya. *Bulletin of the British Museum (Natural History) Geology Supplement*, 1, 1–213.

CUNNINGHAM, J. A., RAHMAN, I. A., LAUTEN-SCHLAGER, S., RAYFIELD, E. J. and DONOGHUE, P. C. J. 2014. A virtual world of palaeontology. *Trends in Ecology & Evolution*, 29, 347–357.

DAUWALDER, P. and REMANE, J. 1979. Etude du banc à nérines à la limite ‘Kimmeridgien’ und ‘Portlandien’ dans le Jura neuchâtelois méridional. *Paläontologische Zeitschrift*, 53, 163–181.

DEFRANCE, M. J. L. 1852. Nerine. *Dictionnaire des Sciences de l’Histoire Naturelle*, 34, 462–464.

DELPY, G. 1940. Les Gastéropodes Mésozoiques de la région Libanaise. *Service des travaux publics, Section d’études géologiques, Notes et Mémôres*, 3, 5–326.

DIETL, G. P., KIDWELL, S. M., BRENNER, M., BURNEY, D. A., FLESSA, K. W., JACKSON, S. T. and KOCH, P. L. 2015. Conservation paleobiology: leveraging knowledge of the past to inform conservation and restoration. *Annual Review of Earth & Planetary Sciences*, 43, 79–103.

DIETRICH, W. 1925. *Gastropoda Mesozoa: fam. Nerineidae*. Fossilium catalogus. 1 Animalia, 31. W. Junk, Berlin, 164 pp.

FAULWWETTER, S., VIJILIEIDAOU, A., KOURATORAS, M., DAILIANIS, T. and ARVANITIDIS, C. 2013. Micro-computed tomography: introducing new dimensions to taxonomy. *ZooKeys*, 263, 1–45.

FISCHER, J.-CL. 1960. Description de quatre espèces nouvelles des genres fossiles Pseudotrochalia Cox et Fibuloptyx Cossmann. *Journal de Conchyliologie*, 99, 201–209.

FÜRSQL, F. T. 1978. The influence of faunal condensation and mixing on the preservation of fossil benthic communities. *Lethaia*, 11, 243–250.

— and PANDEY, D. K. 2003. Sequence stratigraphic significance of sedimentary cycles and shell concentrations in the Upper Jurassic–Lower Cretaceous of Kachchh, western India. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 193, 285–309.

GBIF 2019. Global Biodiversity Information Facility (GBIF). https://www.gbif.org/ [accessed 3 July 2019]

GUERIAU, P., JAVOION, C. and MOCUTA, C. 2018. Show me your yttrium, and I will tell you who you are: implications for fossil imaging. *Palaeontology*, 61, 981–990.

GURALNIK, R. Q. and KURPIUS, J. 2001. Spatial and temporal growth patterns in the phenotypically variable *Littorina saxatilis*: surprising patterns emerge from chaos. 195–228. In ZELDITCH, M. (ed.) *Beyond heterochrony: The evolution of development*. Wiley-Liss.

HAMMER, Ø., HARPER, D. A. T. and RYAN, P. D. 2001. *PAST*: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4, 1–9.

HIRSCH, F. 1980. Jurassic bivalves and gastropods from northern Sinai and southern Israel. *Israel Journal of Earth Sciences*, 28, 128–163.

HSIANG, A.Y., NELSON, K., ELDER, L. E., SIBERT, E. C., KAHANAMOKU, S. S., BURKE, J. E., KELLY, A., LIU, Y. and HULL, P. M. 2018. AutoMorph: accelerating morphometrics with automated 2D and 3D image processing and shape extraction. *Methods in Ecology & Evolution*, 9, 605–612.

JACKSON, I. S. C. and CLAYBOURN, T. M. 2018. Morphometric analysis of inter- and intraspecific variation in the Cambrian helcionelloid mollusc *Mackinnonia*. *Palaeontology*, 61, 761–773.

KARIM, T. S., BURKHALTER, R., FARRELL, Ú. C., MOLINEUX, A., NELSON, G., UTRUP, J. and BUTTS, S. H. 2016. Digitization workflows for paleontology collections. *Palaeontologia Electronica*, 19.3.4T, 1–14.

KERBL, A., HANDSCHUH, S., NÖDL, M. T., METSCHER, B., WALZL, M. and WANNINGER, A. 2013. Micro-CT in cephalopod research: investigating the internal anatomy of a sepolid squid using a non-destructive technique with special focus on the ganglionic system. *Journal of Experimental Marine Biology & Ecology*, 447, 140–148.

KIDWELL, S. M. and BOSENCE, D. W. J. 1991. Taphonomy and time-averaging of marine shelly fauna. 116–209. In ALLISON, P. A. and BRIGGS, D. E. G. (eds). *Taphonomy: Releasing the data locked in the fossil record*. Topics in Geobiology, 9. Plenum Press.
—— and FLESSA, K. W. 1995. The quality of the fossil record: populations, species, and communities. *Annual Review of Ecology & Systematics*, 26, 269–299.

FÜRSICH, F. T. and AIGNER, T. 1986. Conceptual framework for the analysis and classification of fossil concentrations. *Palaios*, 1, 228–238.

KOLLMANN, H. A. 1992. Distribution of gastropods within the Cretaceous Tethyan realm. 95–128. In KOLLMANN, H. A. and HELMUTH, Z. (eds). *New aspects on Tethyan Cretaceous fossil assemblages*. Springer.

—— 2014. The extinct Nerineoidea and Acteonelloidea (Heteroconchae). *Biodiversity & Systematics*, 36, 349.

KOUYOUUMTZAKIS, G. 1989. Les Nerineidae Zittel 1873 (Gasteropoda, Ctenostracana) du Crétacé supérieur sur le pourtour méditerranéen; révision systématique et paléobiogéographique. *Géologie Méditerranéenne*, 16, 17–45.

KRUTA, I., LANDMAN, N. H. and COCHRAN, J. K. 2014. A new approach for the determination of ammonite and nautilid habitats. *PLoS One*, 9, e87479.

LEMANN, R., ZACHOW, S., FUSSEIS, F. and HOFFMANN, R. 2015. A new approach using high-resolution computed tomography to test the buoyant properties of chambered cephalopod shells. *Paleobiology*, 41, 313–329.

—— KORN, D., ZACHOW, S., RYBACKI, E. and HOFFMANN, R. 2016. The evolution and development of cephalopod chambers and their shape. *PLoS One*, 11, e0151404.

LESHNO AFRIAT, Y., EDELMAN-FURSTENBERG, Y., RABINOVICH, R., TODD, J. A. and MAY, H. 2020. Taxonomic identification using virtual palaeontology and geometric morphometrics: a case study of Jurassic nerineoidean gastropods. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.7m0cfpx4

LUKENEDER, A., LUKENEDER, S. and GUSENBAUR, C. 2014. Computed tomography and laser scanning of fossil cephalopods (Triassic and Cretaceous). *Denisia*, 32, 81–92.

MACLEOD, N. 2007. Automated taxon identification in systematics: Theory, approaches and applications. CRC Press, 339 pp.

—— BENFIELD, M. and CULVERHOUSE, P. 2010. Time to automate identification. *Nature*, 467, 154–155.

MOLINEUX, A., SCOTT, R. W., KETCHAM, R. A. and MAISANO, J. A. 2007. Rudist taxonomy using X-ray computed tomography. *Palaeontologia Electronica*, 10, 1–6.

MONNET, C., ZOLLIKOFER, C., BUCHER, H. and GOUDEMAND, N. 2009. Three-dimensional morphometric ontology of mollusc shells by micro-computed tomography and geometric analysis. *Palaeontologia Electronica*, 12, 1–13.

NELSON, G. and ELLIS, S. 2018. The history and impact of digitization and digital data mobilization on biodiversity research. *Philosophical Transactions of the Royal Society B*, 374, 1–15.

PCHELEINTSEV, V. V. 1960. Superfamily Murchisoniacea. In PCHELEINTSEV, V. V. and KOROBKOV, I. A. (eds). *Fundamentals of palaeontology, Mollusca-Gastropoda*. Governmental Technical-Scientific Printing Company, Moskwa, 360 pp.

—— 1965. *Mesozoic Murchisoniata from the strata of the Crimean mountains*. Science Publishing House, Nauka, Moskwa, 216 pp.

RAHMAN, I. A. and SMITH, S. Y. 2014. Virtual palaeontology: computer-aided analysis of fossil form and function. *Journal of Palaeontology*, 88, 633–635.

RAMIREZ, M. J., CODDINGTON, J. A., MADDOSSON, W. P., MIDFORD, P. E., PRENDINI, L., MILLER, J., GRISWOLD, C. E., HORMIGA, G., SIERWALD, P., SCHARFF, N., BENJAMIN, S. P., WHEELER, W. C. and PAGE, R. 2007. Linking of digital images to phylogenetic data matrices using a morphological ontology. *Systematic Biology*, 56, 283–294.

SCOTSE, C. R. 2016. PALEOMAP PaleoAtlas for GPlates and the PaleoData Plotter Program, PALEOMAP Project. https://www.earthbyte.org/paleomap-paleoatlases-gplates

SIRNA, G. 1995. The Nerineids: taxonomy, stratigraphy and paleoecology with particular references to Italian examples. *Geologica Romana*, 31, 285–305.

—— and MASTROIANNI, F. 1993. Jurassic-Cretaceous nerineoids of Campoli Appennino (Latium). *Geologica Romana*, 29, 139–153.

SMITH, U. E. and HENDRICKS, J. R. 2013. Geometric morphometric character suites as phylogenetic data: extracting phylogenetic signal from gastropod shells. *Systematic Biology*, 62, 366–385.

SOHL, N. F. 1987. Presidential address: cretaceous gastropods: contrasts between Tethys and the temperate provinces. *Journal of Palaeontology*, 61, 1085–1111.

SUTTON, M. D. 2008. Tomographic techniques for the study of exceptionally preserved fossils. *Proceedings of the Royal Society B*, 275, 1–7.

—— RAHMAN, I. A. and GARWOOD, R. J. 2014. Techniques for virtual palaeontology. John Wiley & Sons Ltd, 200 pp.

SUTTON, M., RAHMAN, I. and GARWOOD, R. 2016. Virtual palaeontology—an overview. *The Palaeontological Society Papers*, 22, 1–20.

TAFFOREAU, P., BOISTEL, R., BOLLER, E., BRAVIN, A., BRUNET, M., CHAIMANEE, Y., CLOETENS, P., FEIST, M., HOSZOWSKA, I., JAEGER, J. J., KAY, R. F., LAZZARI, V., MARIVAUX, L., NEL, A., NEMOZ, C., THIBAULT, X., VIGNAUD, P. and ZABLER, S. 2006. Applications of X-ray synchrotron microtomography for non-destructive 3D studies of palaeontological specimens. *Applied Physics A*, 83, 195–202.

TAJIK, A., MORIMOTO, N., WANI, R., NAGLIK, C. and KLUG, C. 2015. Intraspecific variation of phragmocone chamber volumes throughout ontogeny in the modern nautilid *Nautilus*. *PeerJ*, 3, e1306.

—— and KLUG C. 2018. Intraspecific variation in cephalopod conchs changes during ontogeny: perspectives from three-dimensional morphometry of *Nautilus pompilius*. *Paleobiology*, 44, 118–130.

TANABE, K., MISAKI, A., LANDMAN, N. H. and KATO, T. 2013. The jaw apparatuses of Cretaceous Phylloceratina (Ammonoidea). *Lethaia*, 46, 399–408.

TRACEY, S., TODD, J. A. and ERWIN, D. H. 1993. *Mollusca, Gastropoda*. 131–167. In BENTON, M. J. (ed.) *The fossil record 2*. Chapman & Hall.
VAUGHAN, P. G. 1988. *Cretaceous Nerineaceous gastropods: Systematics, affinities and palaeoecology*. Open University, 264 pp.

WAITE, R., WETZEL, A., MEYER, C. A. and STRASSER, A. 2008. The palaeoecological significance of nerineoid mass accumulations from the Kimmeridgian of the Swiss Jura Mountains. *Palaios*, 23, 548–558.

WENZ, W. 1938–1944. Allgemeiner teil und prosobranchia. 816–831. In SCHINDEWOLF, O. H. (ed.) *Handbuch der paläozoologie*. Vol. 6. Gebr. G. Bornträger, Berlin.

WIECZOREK, J. 1975. The taxonomy and life environment of the Upper Jurassic nerineid gastropods from the genus *Fibulopygmatis* Pchelintsev (1965). *Acta Geologica Polonica*, 25, 153.

---

WIECZOREK, J. 1979. Upper Jurassic nerineaceous gastropods from the Holy Cross Mts (Poland). *Acta Palaeontologica Polonica*, 24, 299–350.

---

ZITTEL, K. A. 1873. Paläontologische Studien über die Grenzschichten der Jura- und Kreideformation. 3. Die Gastropoden der Stramberger Schichten. *Paläontologische Mitteilungen aus dem Museum des Königlich Bayerischen Staates*, 2, 311–490.

ZITTEL, K. A. 1873. Paläontologische Studien über die Grenzschichten der Jura- und Kreideformation. 3. Die Gastropoden der Stramberger Schichten. *Paläontologische Mitteilungen aus dem Museum des Königlich Bayerischen Staates*, 2, 311–490.

---

ZELDITCH, M. L., SWIDERSKI, D. L., SHEETS, H. D. and FINK, W. L. 2004. *Geometric morphometrics for biologists: A primer*. Elsevier/Academic Press, 416 pp.