Muscles and muscle scars in fossil malacostracan crustaceans

Adiël A. Klompmaker, Matuš Hyžný, Roger W. Portell, Clément Jauvion, Sylvain Charbonnier, Shane S. Fussell, Aaron T. Klier, Raymond Tejera, Sten L. Jakobsen

Abstract

Exceptionally preserved specimens yield critical information about the soft-part anatomy and the evolution of organisms through time. We compiled the first global dataset of exceptionally preserved muscles in malacostracans consisting of 47 occurrences, including 18 new records, predominantly preserved in Mesozoic Konservat-Lagerstätten (>70% of occurrences). Early diagenetic mineralization through phosphatization is the dominant process for exceptional preservation of muscles in malacostracans. Over 70% of taxon occurrences with muscles preserved are compressed. Rarer, three-dimensionally preserved specimens allow more detailed study of muscles. One example are specimens of the mid-Holocene ghost shrimp *Sergio* sp. from Panama, showing exquisitely preserved strings of muscle fibers attached to the shell interior, resembling the muscle arrangement of modern ghost shrimps. Other fossil malacostracans, including the oldest known fossil shrimp, also show musculature similar to modern taxa. We hypothesize that this muscle conservatism may be related to the confined space within the malacostracan shell in conjunction with the relatively stable body plan of several clades. We also assembled the first dataset on muscle attachment scars in malacostracans. Unlike muscles, muscle scars are more common. Approximately 24% of the 357 articles analyzed yielded evidence of muscle scars, but such scars were only recognized for 19% of the 162 taxon occurrences that showed muscle scars. Muscle scars are common from the Late Jurassic onwards, are found primarily in Brachyura and Axiidea, and do not suffer from a Lagerstätten-effect. Rocks with well-preserved specimens should yield an additional wealth of information on the soft part anatomy of malacostracans. Similarly, muscle scars represent an almost untapped, complementary source of information on muscle evolution.

1. Introduction

The preservation of soft tissues in fossils provides exceptional insight into the biology of ancient metazoans. Muscles have been used to infer the functioning of organisms, their taxonomic identity, and evolutionary relationships among clades (e.g., Bergström et al., 1989; Kaji et al., 2018; Parry et al., 2015; Trinajstic et al., 2007; Young and Vinther, 2017). Muscles are preserved in a variety of arthropods (e.g., Briggs et al., 2005; Hu et al., 2017; Siveter et al., 2010; Vannier et al., 2014), including in multiple clades of Malacostraca (e.g., Beurlen, 1930; Feldmann and Schweitzer, 2010; Wilby and Briggs, 1997). The most diverse clade among malacostracans are the Decapoda, with a fossil record of ~3700 species (Schweitzer and Feldmann, 2016) and major species- and genus-level diversifications from the Mesozoic onwards (Klompmaker et al., 2013; Schweitzer and Feldmann, 2015; Sepkoski, 2000). Other, less diverse malacostracan clades with a macrofossil record are Isopoda, Phyllocarida, and Hoplocarida. Muscles in fossil malacostracans are almost exclusively mentioned as part of systematic descriptions thus far, but have the potential to provide insight into the evolution of myoanatomy through time.

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Muscle attachment traces or scars on the hard parts of fossil metazoa can provide complementary information on many aspects of metazoan biology in deep time. Muscle scars have helped gain insight into the evolution of digestive tracts, the function of skeletal elements, the size of soft tissues, life habit, and the relatedness among organisms (e.g., Doguzhaeva and Mutvei, 1991; Dzik, 2010; Knight and Morris, 2019; Kröger and Mutvei, 2005; Lerosey-Aubril and Peel, 2018; Richter and Fischer, 2002; Topper and Skovsted, 2017). Such scars have been found in fossil malacostracans (e.g., Glaessner, 1960; Hof and Schram, 2002; Fischer, 2010; Doguzhaeva and Mutvei, 1991; Dzik, 2010; Knight and Morris, 2019; Kröger and Mutvei, 2005; Lerosey-Aubril and Peel, 2018; Richter and Fischer, 2002; Topper and Skovsted, 2017). Such scars have been found in fossil malacostracans (e.g., Glaessner, 1960; Hof and Schram, 1998; Schweigert and Koppka, 2011), but, again, they are primarily mentioned as part of taxon descriptions.

Here we review muscles and muscle scars in fossil malacostracans to evaluate (1) muscle preservation through geologic time based on known and new occurrences, (2) how fossil muscles compare to those in extant representatives, (3) the taxa with muscle attachment scars and their location, and (4) the frequency and the degree of recognition of muscle scars.

Institutional abbreviations. GBA: Geologische Bundesanstalt, Vienna, Austria; MAB: Oertijdmuseum, Boxtel, The Netherlands; MGUH: Natural History Museum of Denmark, Geological Museum, University of Copenhagen, Denmark; MNHN: Muséum national d’Histoire naturelle, Paris, France; NHMW: Department of Geology and Palaeontology, Natural History Museum Vienna, Austria; SMF: Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; UF: Florida Museum of Natural History at the University of Florida, Gainesville, USA; UMJPA: Geological-palaeontological Department, Universalmuseum Joanneum, Graz, Austria.

2. Major muscle groups and muscle scars of extant malacostracans with a fossil record

Skeletal muscles coupled with the nervous system provide the necessary equipment for organisms to actively move. The neuromuscular morphology in malacostracans is responsible for distinct ways of motion, including swimming, tail-flipping (e.g., escape response, see Heitler et al., 2000), digging, and burrowing. Skeletal muscles in the body regions and the appendages are generally organized into antagonistic pairs, such as extensor/flexor, levator/depressor, and promotor/remotor muscle pairs. Skeletal muscles work against a mechanical system of levers formed by the exoskeleton, apodemes, and joints of the segments; the movement of appendages results from combinations of movements of several joints (Evoy and Ayers, 1982). Muscles in malacostracans typically are striated muscles, with actin and myosin filaments. The fiber type, whether fast (phasic), slow (tonic) or intermediate, in homogenous muscles is largely genetically determined (Wahle et al., 2012).

2.1. Thoracic muscles

Thoracic muscles (Fig. 1) provide support for the animal body and interconnect body parts such as the thorax and pleon. The thorax in decapods is rather inflexible and contains mainly thoracopleonal muscles, in addition to those connecting the internal with the external skeleton (Glaessner, 1969). Nevertheless, the thoracic musculature is extraordinarily complex and the number of individual muscles is large in lobsters and most anomurans, whereas the whole arrangement in brachyurans is less complicated (Pilgrim, 1973). In hoplocarids, the thorax is more flexible and contains also bundles of flexors and extensors (Pilgrim, 1964). In decapods, various paired bundles of dorsal thoracic muscles are situated either between the inner side of the carapace and the endophragmal skeleton or between elements of the endophragmal skeleton (Keiler et al., 2016). The attachment areas of muscles are recognizable on the inner surface of the carapace (Glaessner, 1960, 1969).

In decapods, the most important groups of muscles attached to the carapace are the epimeral attractor muscle (muscle inserting along the branchiocardiac groove that connects the epimeral wall of the ventral thorax to the dorsal carapace), mandibular muscles (operating mandibles), gastric muscles (responsible for moving the gastric mill), and a small portion of the thoraco-pleonal muscles (interconnecting thorax with pleon). Ventral thoracic muscles are extrinsic muscles (flexors + extensors) of the bases of appendages and are located directly above the sternum (Keiler et al., 2016). There is considerable variation in the development of mandibular muscles. In lobsters, the posterior (adductor) muscle is very strong and its area of attachment covers a large part of the lateral internal surface of the carapace. In squat lobsters and crab-like decapods, this muscle is very weak and the lateral adductor muscle occupies more space on its surface (Glaessner, 1960).

Of the external gastric muscles, only the group of the posterior muscles is attached to the carapace. It is connected with two small calcareous projections of its apodemes close to the median line of the carapace and recognizable from the outside as a pair of minute pits, also called gastric pits. The anterior gastric muscles are attached to the lower surface of the rostrum; in brachyurans, crabs, they are attached to small flat calcareous projections underneath the epigastric regions of the carapace.

2.2. Pleonal muscles

Within malacostracan pleons (Figs. 2–3), there are dorsal extensor muscles that straighten the pleon and larger ventral flexor muscles (Herrick, 1909) that are responsible for swimming in shrimps (Onnen and Zebe, 1983) and the effective stroke of the “tail flip” escape
response (caridoid escape reaction, typical for shrimps and lobsters). Dorsal, ventral, and lateral pleonal muscles are recognized depending on their position. The dorsal pleonal muscles belong to the extensor and the ventral muscles to the flexor system of the pleon (Herrick, 1909; Huxley, 1880; Keiler et al., 2017; Young, 1959). The lateral muscles are relatively thin, fan-shaped, and apparently function to retain the position of the cuticle during movements of the animal (Young, 1959). The pleonal muscles are bilaterally symmetrical in most malacostracans, except in hermit crabs and their relatives (Glaessner, 1969; McLaughlin, 1980; Pilgrim, 1973).

The pleonal muscles differ greatly between the higher malacostracan taxa. They are most pronounced in stomatopods, shrimps, and lobsters, occupying most of the pleon. In astacidean lobsters, the pleon contains strong muscular bundles. Well-developed musculature of the sixth pleomere and telson in astacideans (Herrick, 1909) is used in rapid escape flexions of the pleon and tail fan. The pleonal musculature is similar in axiideans and gebiideans, except for the absence of the ventral telsonal flexor muscles (Paul et al., 1985). The arrangement of

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**Fig. 2.** Thoracic and pleonal muscles in decapod crustaceans. A. Thoracic and pleonal musculature in lobsters as exemplified in an astacid crayfish (redrawn from Schmidt, 1915: Fig. 1). B. Muscles of the telson and the sixth pleonal segment in lobsters and shrimps (redrawn from Paul et al., 1985: Fig. 1). Top = cambarid crayfish; middle = upogebiid mud shrimp; bottom = pandalid caridean shrimp. Left column = axial muscles; right column = appendage muscles. C. Transverse section through the fourth pleonal segment in the squat lobsters *Munida Leach, 1820*, (top) and *Galathea Fabricius, 1793*, (middle) and a porcelain crab *Petrolisthes Stimpson, 1858*, (bottom) (redrawn from Keiler et al., 2017: Fig. 13).
the sixth pleonal and telson neuromusculature in axiideans and gebii-deans is considered a secondary adaptation to their burrowing behavior (Dworschak et al., 2012). A reduction of pleonal and tailfan muscles is observed in most anomurans (Keiler et al., 2015, 2016, 2017). The proportional volume of pleonal and tailfan musculature is even lower in crab-like (carcinized) anomurans and in brachyurans.

2.3. Walking leg muscles

The muscles of the walking legs (thoracic appendages) are attached to the internal (endophragmal) skeleton and do not reach the carapace (Glaessner, 1960) (Fig. 4B). The musculature of walking legs is complex but highly conserved (Abrahameczik-Scanzoni, 1942; Vidal-Gadea and Belanger, 2009). Proximal muscles originate from the endophragmal skeleton and its mass relative to the distal musculature is limited (Vidal-Gadea and Belanger, 2009). In malacostracans, pereopods typically consist of six segments. For muscles in distal segments, all but two muscles have common features between the different pereopods. In most cases, the pereopod segments articulate via bicondylar joints, restricting the range of motion of each segment to a single plane. The relatively simple muscle arrangement consists of openers, closers, stretchers, benders, extensors, flexors, and reductors (Vidal-Gadea and Belanger, 2009).

Fig. 3. Pleonal muscles in the stomatopod Squilla empusa Say, 1818. Modified from Hessler (1964: Fig. 44) and redrawn Moore and McCormick, 1969: Fig. 29.

Fig. 4. Pereopod muscles in decapod crustaceans. A. Apodemes of a brachyuran claw. B. Dorsal view of the distal musculature of a walking leg (top) and a cheliped (bottom) of a majoid crab (redrawn from Vidal-Gadea and Belanger, 2009: Fig. 2). C. Inner and outer sides of the cheliped of the extant ghost shrimp Gourerna phuketensis Sakai, 2002, (SMF 29520) showing muscle bundles arranged in a reticulate pattern through the translucent cuticle (from Hyžný and Klompmaker, 2015: Fig. 8A–B).
2.4. Cheliped muscles

The claw represents a relatively simple motor system with only two antagonistic muscles, an opener (abductor) and a closer (adductor), which control the movements of the dactylus (Huxley, 1880; Kaji et al., 2018; Pillai, 1990) (Fig. 4A, C). Decapod claws in heterochelous taxa often differ in the type of muscle fibers. Average sarcomere length determines whether muscle fibers are slow- or fast-moving; muscles with a shorter sarcomere length tend to be faster in their contraction. The major (crusher) claw is stout and its closer muscle is composed of slow fibers, so the claw closes strongly but slowly, whereas the minor (cutter) claw is slender and closes very rapidly (Govind et al., 1987); its closer muscle is made up of predominantly fast fibers and a small ventral band of slow fibers. However, sarcomere length undergoes changes during development (Govind et al., 1987). In fact, differentiation of fiber type in lobster claws occurs during the post-larval period, resulting in an asymmetrical ganglion development that gives rise to a major claw with exclusively slow fibers and a cutter claw with predominantly fast fibers (Wahle et al., 2012, and references therein). The closer muscle in the paired claws of lobsters, crayfishes, and malacostracans are relatively well-known. Consequently, the conditions under which muscles can preserve suitable soft tissues, even though they are among the most decay-prone parts (Parry et al., 2018), When preserved, they are often phosphatized (e.g., Briggs et al., 1993; Trinajstic et al., 2007; Wilby et al., 1996; Wilson et al., 2016), but sometimes silicified (Robin et al., 2018) or preserved in carbonates (Briggs et al., 1997). Phosphatization is the most common type of muscle preservation, which has been thoroughly explored and reproduced in taphonomic experiments (Briggs et al., 1993; Briggs and Kear, 1994, 1993; Kear et al., 1995; Sagemann et al., 1999). These experiments show that extensive and high-quality phosphate muscle preservation (mineral morphology replication) is mainly driven by a few interconnected factors: favoring conditions include a high microbial activity, a low pH, and high ion availability. One of the most prominent and, hence, to a large extent, the respective muscle scars on the propodal surface. We hypothesize that the surface area of the closer muscle scars on the lateral surfaces of the cheliped propodus may be positively correlated with the force of the claw. Muscles in arthropods in general are mechanically linked to the epidermis and cuticle by a complex network of cytoskeletal and junctional elements (Žnidaršič et al., 2012), and these can be expressed as the muscle scars on cuticular surfaces. The fibers of the muscle attachments go through the cuticle; the fibers traverse the entire new cuticle during the molting process, and extend from the tendon cell apex up to the exocuticular layer in the old cuticle (Žnidaršič et al., 2012). Unfortunately, data on how the muscle attachment sites change the properties of the crustacean cuticle are very limited (see Buchholz and Buchholz, 1989; Yamada and Keyser, 2009; Žnidaršič et al., 2012).

3. Muscles

3.1. Processes of muscle preservation

Muscles in metazoans are among the most commonly preserved soft tissues, even though they are among the most decay-prone parts (Parry et al., 2018). When preserved, they are often phosphatized (e.g., Briggs et al., 1993; Trinajstic et al., 2007; Wilby et al., 1996; Wilson et al., 2016), but sometimes silicified (Robin et al., 2018) or preserved in carbonates (Briggs et al., 1997). Phosphatization is the most common type of muscle preservation, which has been thoroughly explored and reproduced in taphonomic experiments (Briggs et al., 1993; Briggs and Kear, 1994, 1993; Kear et al., 1995; Sagemann et al., 1999). These experiments show that extensive and high-quality phosphate muscle preservation (mineral morphology replication) is mainly driven by a few interconnected factors: favoring conditions include a high microbial activity, a low pH, and high ion availability. One of the most prominent factors controlling phosphatization is pH: in a closed, lower pH (micro) environment, phosphates tend to form, whereas in an open, more alkaline environment carbonate precipitation dominates (Briggs and Wilby, 1996; Sagemann et al., 1999). Three-dimensional preservation of soft tissues, including muscles, is most frequently found in combination with phosphatization (Allison and Briggs, 1991). Several taphonomic experiments have been conducted on malacostracans (Briggs and Kear, 1994; Hof and Briggs, 1997; Klompmaker et al., 2017; Table 1; Sagemann et al., 1999). Consequently, the conditions under which muscles can preserve in malacostracans are relatively well-known.
Table 1
All malacostracan taxa with muscles preserved based on the literature and new records arranged by age. * indicates that specimen(s) of this taxon were previously studied in the accompanying paper, but muscles are reported here for the first time. § Taxon may be conspecific to the taxon in the following row (see Schweigert, 2001).

<table>
<thead>
<tr>
<th>Clade</th>
<th>Taxon</th>
<th>Locality</th>
<th>Stratigraphic unit</th>
<th>Preservation specimen: compressed (C) or three-dimensional (3D)</th>
<th>Preservation process</th>
<th>Konservat-Lagerstätte?</th>
<th>Age (young to old)</th>
<th>Part with muscle preserved</th>
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<td>Sergio sp.</td>
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<td>–</td>
<td>3D</td>
<td>Phosphatization</td>
<td>No</td>
<td>mid-Holocene</td>
<td>Major cheliped propodi</td>
<td>herein</td>
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<td>Pinnixa sp.</td>
<td>Cape Blanco, Oregon, USA</td>
<td>–</td>
<td>3D</td>
<td>Phosphatization</td>
<td>No</td>
<td>Late Pleistocene</td>
<td>Venter</td>
<td>Zullo and Chivers (1969)</td>
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<td>Squilla aurantium Ahyong et al., 2013</td>
<td>Taulliguan (La Croix de Bouchet), France</td>
<td>–</td>
<td>Compressed</td>
<td>Phosphatization</td>
<td>No</td>
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<td>Pleon</td>
<td>Ahyong et al. (2013); pers. comm. Carolin Haug 25 April 2017</td>
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<td>Gebiidea</td>
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<td>Kamloops Gr, McAbee beds</td>
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<td>Phosphatization</td>
<td>Y</td>
<td>Eocene (Ypresian)</td>
<td>Shadows of muscle in propodus and pleon</td>
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<td>Aegur sp.</td>
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<td>Sahel Alma</td>
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<td>Y</td>
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<td>Pleon</td>
<td>*Charbonnier et al. (2017)</td>
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<td>Y</td>
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<td>Y</td>
<td>Middle Jurassic (Callovian)</td>
<td>Carapace and pleon</td>
</tr>
<tr>
<td>Polychelida</td>
<td><em>Proeryon giganteus</em> (Van Straelen, 1923)</td>
<td>La Voulte-sur-Rhône, France</td>
<td>La Voulte-sur-Rhône Lagerstätte</td>
<td>Compressed and 3D</td>
<td>Y</td>
<td>Middle Jurassic (Callovian)</td>
<td>Carapace and pleon</td>
</tr>
<tr>
<td>Polychelida</td>
<td><em>Willemeioscoria ovalis</em> (Van Straelen, 1923)</td>
<td>La Voulte-sur-Rhône, France</td>
<td>La Voulte-sur-Rhône Lagerstätte</td>
<td>3D</td>
<td>Y</td>
<td>Middle Jurassic (Callovian)</td>
<td>Carapace and pleon</td>
</tr>
<tr>
<td>Polychelida</td>
<td><em>Hellerocaris falloi</em> (Van Straelen, 1923)</td>
<td>La Voulte-sur-Rhône, France</td>
<td>La Voulte-sur-Rhône Lagerstätte</td>
<td>Compressed and 3D</td>
<td>Y</td>
<td>Middle Jurassic (Callovian)</td>
<td>Carapace and pleon</td>
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<tr>
<td>Penaeoidea</td>
<td><em>Archeosolomoea stradmi</em> Carriol and Riou, 1991</td>
<td>La Voulte-sur-Rhône, France</td>
<td>La Voulte-sur-Rhône Lagerstätte</td>
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<td>Y</td>
<td>Middle Jurassic (Callovian)</td>
<td>Carapace and pleon</td>
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<tr>
<td>Penaeoidea</td>
<td><em>Ager brevirostris</em> Van Straelen, 1923</td>
<td>La Voulte-sur-Rhône, France</td>
<td>La Voulte-sur-Rhône Lagerstätte</td>
<td>Compressed and 3D</td>
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<td>Middle Jurassic (Callovian)</td>
<td>Carapace and pleon</td>
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<tr>
<td>Erymida</td>
<td><em>Eryma ventrosum</em> (von Meyer, 1835)</td>
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<td>La Voulte-sur-Rhône Lagerstätte</td>
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<td>Y</td>
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<td>Carapace and pleon</td>
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<tr>
<td>Polychelida</td>
<td><em>Proeryon laticaudatus</em> Beurlen, 1928 (as <em>P. giganteus</em> Beurlen, 1930)</td>
<td>Holzmaden, Germany</td>
<td>Posidonia Shale Fm</td>
<td>Compressed</td>
<td>Y</td>
<td>Early Jurassic (Toarcian)</td>
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<td>indet. shrimp</td>
<td>Osteno, Italy</td>
<td>Lombardische Kieselkalk Fm</td>
<td>Compressed</td>
<td>Phosphatization</td>
<td>Early Jurassic (Sinemurian)</td>
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<td>Bearsden, Glasgow, Scotland</td>
<td>Limestone Coal Fm</td>
<td>Compressed</td>
<td>Phosphatization</td>
<td>Carboniferous (Mississippian)</td>
<td>Possible traces of muscles in pleon</td>
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<tr>
<td>Peracarida</td>
<td><em>Teillicaris woodwardi</em> Etheridge, 1877</td>
<td>Guillane, Scotland</td>
<td>Guillane shrimp-bed, Guillane Fm</td>
<td>Compressed</td>
<td>Phosphatization</td>
<td>Carboniferous (Visean)</td>
<td>–</td>
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<td>Aeschropectida</td>
<td><em>Joannella landi</em> Schram and Schram, 1979</td>
<td>Fergus County, Montana, USA</td>
<td>Heath Shale</td>
<td>Compressed</td>
<td>Not mentioned</td>
<td>Carboniferous (Mississippian)</td>
<td>Mandible and pleopod muscles</td>
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<td>Penaeoidea</td>
<td><em>Adcalopoda majori</em> Feldmann and Schweitzer, 2010</td>
<td>Ryan Quarry, Oklahoma, USA</td>
<td>Woodford Shale</td>
<td>Compressed</td>
<td>Phosphatization</td>
<td>Late Devonian (Famennian)</td>
<td>Pleon</td>
</tr>
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<td>Phyllocarida</td>
<td><em>Montezicaris gogoensis</em> Briggs et al., 2011</td>
<td>Locality 92, Canning Basin, Western Australia</td>
<td>Gogo Fm</td>
<td>Compressed</td>
<td>Phosphatization</td>
<td>Middle-Late Devonian (Givetian-Famennian)</td>
<td>4carapace</td>
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<td>Phyllocarida</td>
<td><em>Nahecaris staertzi</em> Bergström et al., 1987</td>
<td>Hunsrück and Taunus regions, Germany</td>
<td>Hunsrück Slate</td>
<td>Compressed</td>
<td>Pyritization</td>
<td>Early Devonian</td>
<td>Carapace adductor muscle scar</td>
</tr>
<tr>
<td>Phyllocarida</td>
<td><em>Ceratocaris winnesheickensis</em> Briggs et al., 2015</td>
<td>Site on the Upper Iowa River, Iowa, USA</td>
<td>Winneshiek Lagerstätte</td>
<td>Compressed</td>
<td>Phosphatization</td>
<td>Middle Ordovician (Darienwalian)</td>
<td>Posterior carapace and anterior pleon</td>
</tr>
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3.2. Muscle preservation through time per malacostracan clade

After a comprehensive search of the literature for muscles preserved in malacostracans supplemented with new occurrences, we report a total of 47 occurrences. Most of them originate in the Jurassic and Cretaceous (Fig. 5; Table 1). Most occurrences are from Konservat-Lagerstätten, which is not surprising because such Lagerstätten are defined based on the presence of soft tissues and well-articulated specimens (Seilacher, 1970). Most occur in the three malacostracan-rich Lagerstätten: the Middle Jurassic of La Voulte-sur-Rhône in France (e.g., Charbonnier et al., 2014), the Late Cretaceous of Sahel Alma in Lebanon (e.g., Charbonnier et al., 2017), and the Late Jurassic of Solnhofen in Germany (e.g., Garassino and Schweigert, 2006). Due to this Lagerstätten-effect, trends through time in muscle occurrences do not reflect diversity patterns. For example, decapod crustaceans first became diverse in the Late Jurassic (Klompmaker et al., 2013), but their diversity continued to rise into the Cenozoic (Schweitzer and Feldmann, 2015; Sepkoski, 2000), from which relatively few occurrences of muscle preservation are known. Marine, malacostracan-bearing Lagerstätten are primarily known from the Mesozoic.

Most malacostracans with muscles preserved are Decapoda, but muscles are also known from phyllocarids and hoplocarids (including stomatopods and aeschronectids). Within decapods, brachyurans or true crabs became the dominant clade beginning in the latest Cretaceous (Klompmaker et al., 2013; Schweitzer and Feldmann, 2015), but they are scarcely represented in our list of muscle occurrences (Fig. 5; Table 1). Brachyurans first became abundant in the Late Jurassic, predominantly found in coral- and sponge-associated habitats (Klompmaker et al., 2013; Krobicki and Zatoń, 2008). However, they are rarely found in the Tithonian Solnhofen Lagerstätte in southern Germany (Feldmann et al., 2016), close to coral- and sponge-associated habitats inhabited by many brachyurans (e.g., Schweitzer and Feldmann, 2009; Wehner, 1988). Likewise, brachyurans are also absent in the Callovian La Voulte-sur-Rhône Lagerstätte in France (Charbonnier et al., 2014: Table 1), but time-equivalent crabs are found in oolitic limestones in France (Crônier and Boursicot, 2009). Although brachyurans are more common in Cretaceous Lagerstätten (e.g., Charbonnier et al., 2017; Klompmaker, 2013: Appendix A; Larghi, 2004), they still do not dominate decapod assemblages.
3.3. Types of muscle preservation

Most muscles are preserved in compressed specimens rather than in 3-dimensionally (3D) preserved specimens (Fig. 6). Most of the 3D-preserved occurrences are from the La Voulte-sur-Rhône Lagerstätte, whereas other occurrences of that Lagerstätte were represented by both compressed and 3D-preserved specimens. Other 3D-preserved specimens with muscle are found primarily in the Cenozoic (Zullo and Chivers, 1969; herein). The muscles in the compressed specimens consist predominantly of re-mineralized muscles and sometimes outlines of muscles (e.g., Feldmann et al., 2011). Muscles in malacostracans are primarily preserved through phosphatization (Table 1).

3.4. Location of preserved muscles

Preserved muscles are most frequently found in the pleon (27/47 occurrences), whereas they occur less often in appendages (9/47) and in the carapace/cephalothorax (13/47). The pleons of malacostracans including Penaeoidea, Polychelida, and Stomatopoda contain primarily muscles for swimming and other movement purposes (e.g., Hertzler and Freas, 2009; Vogt, 2002; Fig. 2). Conversely, the carapace of malacostracans contains a variety of other tissues as well (Davie et al., 2015; Warner, 1977; Fig. 1), implying that the pleon contains more muscles proportionally and volumetrically. Therefore, under the assumption of equal preservational potential across muscle groups, muscles preserved in pleons may be found more frequently. However, preservation potential may not be equal for each muscle type as suggested for a phosphatized Cretaceous polychaete (Wilson et al., 2016), but this aspect has not been investigated for malacostracans thus far. Moreover, gut-derived microbes appear to play a key role in the preservation of internal anatomy by consuming tissue but also mediating authigenic mineralization in the branchiopod brine shrimp *Artemia* Leach, 1819, after rupture at the mid- to hindgut junction (Butler et al., 2015). Different guts are found in the carapace to the pleonal region in malacostracans (McGaw and Curtis, 2013). Thus, the position of gut wall rupture may be critical for differential preservation of muscles within an individual in a closed system. However, external microbes may also enter the body cavity in different manners (e.g., mouth, at appendage joints after disarticulation) and could affect muscle preservation.

3.5. Known and new preserved muscles in fossil malacostracans

Most occurrences of muscles in malacostracans have either been figured and mentioned as part of papers focusing primarily on systematics (e.g., Audo and Charbonnier, 2013; Haug et al., 2013; Vega et al., 2007) or are part of papers about a variety of aspects of...
preservation (e.g., Briggs and Kear, 1994; Jauvion et al., 2016). Other papers merely mention but do not show the presence of muscles (Franţescu, 2012). Some of the best figured examples of muscles in fossil malacostracans are shown in Fig. 7.

A survey of material in the collection of the Florida Museum of Natural History (AAK), part of collection of the Muséum National d'Histoire Naturelle (SC, CJ), and part of the collection of the Natural History Museum of Denmark (SLJ) has yielded 18 new taxon occurrences with muscles preserved. While all new occurrences can be found in Table 1, we here highlight a number of particularly well-preserved specimens.

One example are major cheliped propodi from ghost shrimp *Sergio* sp. from the Pacific side of Panama. These specimens originate from the mid-Holocene (5015 ± 50 years BP based on AMS C-14 analysis of the co-occurring bivalve *Lirophora mariae* (d’Orbigny, 1846) [UF 233967]). Multiple specimens show evidence of remineralized muscles of varying quality (Fig. 8A–C). One specimen in particular shows superbly preserved muscles (Fig. 8C–I), one of the best examples in the malacostracan fossil record. Muscles are attached to the inner side of the cuticle (Fig. 8D) and, at the largest scale, are composed of bundles that merge at the point of attachment to the cuticle. These bundles consist of fibers (Fig. 8F) and the individual fibers, in turn, consist of smaller fibers (Fig. 8H). No more details can be seen at even higher magnification (Fig. 8I). Some fibers appear to be surrounded by a sheath-like structure (Fig. 8F, middle left part; Fig. 8G). A microCT scan (Appendix 1) suggests that additional muscles are preserved inside this specimen underneath the cuticle. The muscle remains are phosphatized to hydroxyapatite and/or fluorapatite, whereas the cuticle is composed of magnesian calcite as suggested by a combination of monocrystal x-ray diffraction (Fig. 8A–B) and energy-dispersive x-ray spectroscopy (Fig. 8C–D). The muscle bundles are part of the adductor (closer) muscle, whereas obvious muscles belonging to the opener muscle are not visible (Fig. 8C).

Fig. 9. Monocrystal x-ray diffraction and SEM energy-dispersive x-ray spectroscopy analyses of the muscle and cuticle of the cheliped major propodi of the mid-Holocene ghost shrimp *Sergio* sp. from the Pacific side of Panama (Farfan/Amador beaches). A–B. Monocrystal XRD graphs of the muscle fibers (A) and cuticle (B) of specimen UF 251889. A. Diffractionogram of a muscle fiber microsampling, attributed to hydroxyapatite and/or fluorapatite (peaks noted with a). B. Diffractionogram of a cuticle microsampling, attributed to magnesian calcite (peaks noted with c). C–D. Elemental map produced by an SEM-EDS (energy-dispersive x-ray spectroscopy) showing elevated concentrations of phosphorus indicated by purple dots where mineralized muscle is present, but not on the cuticle present on the very bottom part (specimen UF 251887). The electrons emitted were unable to reach and/or were reflected/emitted so that they were not detected for some deeper parts of the specimen, including the ‘hole’ in the center-right. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)


Fig. 10. Muscles preserved in the fossil dendrobranchiate shrimp *Archeosolenocera straeleni* Carriol and Riou, 1991, from the Middle Jurassic (Callovian) of the La Voulte-sur-Rhône Lagerstätte in France (MNHN.F.A58641). A sagittal polished section was prepared from the pleon to show muscle fibers. A. Entire specimen (photograph by Peter Massicard). B–C. SEM in lens detector image of muscle fibers, muscle fibers in light grey (exact location within pleon not known). C. Magnified image of lower middle part of B.
Other new examples include the dendrobranchiate shrimp *Archeosolenocera straeleni* Carriol and Riou, 1991, from the Middle Jurassic (Callovian) of the La Voulte-sur-Rhône Lagerstätte in France (Fig. 10); the glypheid lobster *Gigacerina saemanni* (Oppel, 1861) from the Late Jurassic (Kimmeridgian/Tithonian) lithographic limestones of the Cerin Lagerstätte, France, and muscles from the extant glypheid lobster *Neoglyphea inopinata* Forest and Saint Laurent, 1975, for comparison. A. Complete fossil specimen MHNL.20015625 in dorso-ventral compression, under UV light. B–C. Close-up of pleonal somites 4 and 5 with strings of muscle fibers. D–E. Close-up of tail fan with strings of muscle fibers in both the basipodite and the proximal region of telson. Abbreviations: bap = basipodite, di = diaeresis, en = uropodal endopod, ex = uropodal exopod, mf = muscle fibers (in blue), pl = pleopods, s4–s6 = pleonal somites 4 to 6, t = telson. F. For comparison, elongated strings of muscle fibers from pleonal somite s6 from the extant glypheid lobster MNHN-IU-2008-14,762 collected by Mission MUSORSTOM 1 (Philippines, N. Lubang Islands). Photographs: C. Lemzaouda, line drawings: S. Charbonnier. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Carpentier et al., 2006).
the Cerin Lagerstätte in France (Fig. 11); and an undetermined fossil stomatopod from the Eocene (Ypresian-Lutetian) Lillebælt Clay Formation of Trelde Næs near Fredericia in Denmark (Fig. 12). In all cases, muscles were found in the pleon, but also in the telson and adjacent basipodite for the glypheid. The longitudinal orientation of the muscles in the glypheid suggest that they represent deep extensor muscles or dorsal pleonal muscles, which may apply too for the dendrobranchiate shrimp, although the precise position of the muscles is not known (see Hertzler and Freas, 2009). The similarly oriented muscles in the stomatopod represent dorsoventral trunk muscles (Fig. 3). The longitudinally oriented muscles in the telson and basipodite of the glypheid may represent the telson flexor or extensor and the uropod rotator or remotor (sensu Vogt, 2002, for a crayfish).

4. Muscle scars

In addition to muscles, muscle scars can give additional information about the presence, shape, and size of the muscles. Muscle scars in the malacostracan fossil record are particularly visible on the inner side of the cuticle where the muscles are attached in a reticulate pattern (Figs. 13–14). However, recurring discoloration of the cuticle in a reticulate pattern may also signify muscle attachment spots on the inside of the cuticle (e.g., Carpentier et al., 2006: Fig. 5C; Hyžný and Klompmaker, 2015: Fig. 8; Rumsey et al., 2016: Fig. 3). Muscle scars have previously been noted from internal molds lacking the cuticle (e.g., Berglund and Feldmann, 1989; Bishop, 1978; Crönier and Boursicot, 2009; Glaessner, 1933, 1960; Schweigert and Kopppka, 2011). We noted that muscle scars have previously been incorrectly referred to as ornamentation because true ornamentation is found only on the cuticle surface, which is usually not the case for muscle scars. These scars are not always present or equally obvious on each internal mold of a species, which may be primarily caused by variable preservation (e.g., Fraaije, 2014: Figs. 7, 11). Muscle scars appear more difficult to spot on smaller specimens.

Scars have been used for the taxonomic placement of species. For example, for the Jurassic crab *Tanidromites* Schweitzer and Feldmann, 2008, distinguishing between species is done partly based on muscle scars (Starzyk, 2013, 2015a, 2016); for the Jurassic–Cretaceous crab *Eodromites* Patrulius, 1959, hepatic pits (= scars of antennar extensor muscle mostly likely, see Glaessner, 1969) were mentioned in the diagnosis of genus (Starzyk, 2015b); and muscle scars in the mesogastric region are part of diagnosis of the Middle Jurassic crab *Homolus* Eudes-Deslongchamps, 1835 (Schweitzer and Feldmann, 2010).

Despite the presence of muscle scars in many malacostracan taxa, they have not been studied systematically. Glaessner (1969: R407–R409) in the Treatise of Invertebrate Paleontology on Decapoda indicated that muscle scars deserve more detailed comparative study, but no such studies have been performed thus far.

To explore first-order patterns of muscle scars in fossil malacostracans, we surveyed the published literature from 2004 to 2006 and 2014 to 2016 (357 articles in total) to obtain a reasonable sample size for this century. We searched manuscript texts containing fossil specimens’ images for referrals to muscle scars and we checked for scars in the provided figures. Posterior gastric pits as an attachment for the stomach muscle (Glaessner, 1969; McLaughlin, 1980) and other pits as possible attachment places of muscles are not included in this search because they cannot be observed consistently in the provided figures. We found that muscle scars are present from the Devonian onward and become more common starting in the Jurassic (Fig. 15; Appendix 2), coinciding with the first major species-level diversification of decapods (Klompmaker et al., 2013). The 162 occurrences of malacostracans showing muscle scars is a minimum estimate because we did not

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Fig. 12. Pleon of an undetermined fossil stomatopod (MGUH 32025) from the Eocene (Ypresian-Lutetian) Lillebælt Clay Formation of Trelde Næs near Fredericia, Denmark, with muscles preserved. A. Entire specimen. B–C. Closeups of one of the pleonal segments with muscle fibers.
include ambiguous muscle scars and not all images were of adequate quality to check for muscle scars. There is no preferred rock type in which muscle scars are found; when malacostracans are preserved as internal molds, muscle scars can be found.

Muscle scars are predominantly found on the inner and outer sides of primarily cheliped (first pereopod) propodi of Axiidea, at the base of the mesogastric region of primarily Brachyura, on the anterior gastric region of paguroid anomurans, and lateral to the cardiac region for Brachyura (Appendix 2). These scars represent attachments for the closer or opener muscle, the posterior gastric muscle, the anterior gastric muscle, and the attractor epimeralis muscle, respectively (Figs. 1–4).

Brachyura, Axiidea, and Anomura comprise most of the muscle scar occurrences (Fig. 16A; Appendix 2). Except for one phyllocarid...
occurrence, muscle scars were absent in non-decapod malacostracans such as Isopoda and Stomatopoda, but the number of published articles on fossil representatives of clades was also limited. Whether muscle scars are less common in these clades requires more research, but muscle scars have been mentioned from a Miocene stomatopod (Hof and Schram, 1998: p. 328). Muscle attachments can be seen through the cuticle in some recent isopods (Bruce and Bussarawit, 2004: Fig. 5; Poore and Storey, 2009: Fig. 1A). Therefore, fossil isopods with muscle scars may be expected with targeted research, but we have not been able to find such instances thus far.

Although muscle scars in fossil malacostracans have been known for a long time (e.g., Glaessner, 1933), they are not often recognized to the present day. Of the 162 malacostracan occurrences with muscle scars, only 30 (19%) were specifically mentioned in the text (Fig. 16B; Appendix 2). Most of such occurrences are found in systematic palaeontology articles, for which the description and interpretation of all morphological features including muscle scars is one of the main goals. However, muscle scars were not mentioned for 132 of the occurrences (81%), including 67 occurrences (41%) for which the respective taxa were described, which implies that muscle scars were not recognized. We strongly recommend including muscle scars in taxonomic descriptions. In contrast, 65 muscle scar occurrences (40%) were part of papers that did not describe the respective taxa. It is no surprise that the muscle scars were not mentioned in these cases.

To evaluate the commonness of muscle scars in the fossil malacostracan literature, we surveyed the same 357 articles for the presence of muscle scars. Muscle scars were present in 24% (87) of the articles (Fig. 16C; Appendix 3), indicating that muscle scars are common. This percentage is a minimum estimate because not all images were of sufficient quality to determine whether muscle scars were present. The number of muscle scar occurrences and the percentage of papers with muscle scars jointly suggest that evidence for muscle scars is ubiquitous and provides the opportunity to study large-scale patterns of muscle evolution and attachment.

The patterns of skeletal calcification affecting the likelihood of muscle scar preservation are unexplored. It may be possible that very prominent muscle scars on fossil cheliped propodi of ghost shrimps are associated with a rather thin cuticle, whereas the absence of muscle scars in the fossil lobster chelae may be related to their strong calcification and ornamentation. Alternatively, the depth of the muscle scars on the inside of the cuticular layers may play a role in the preservation of muscle scars. In durophagous brachyuran crabs, the muscle scars are very prominent also in strongly calcified chelae, which may be related to their extreme claw strength (Koslowski and Allmon, 2015; Schenk and Wainwright, 2001; Taylor, 2000).

5. Brief comparison of fossil and modern muscles and muscle scars

Although not all muscle groups are preserved in the specimens figured herein, many of the muscles resemble those found in extant representatives. Of the two best preserved individuals, the position and the pattern of cylindrical bundles of the closer muscle in the mid-Holocene Sergio sp. (Fig. 8) is very reminiscent of those of modern callianassid ghost shrimp (Fig. 4C). Much more remarkable is the strong similarity of the pleonal muscles of the Late Devonian penaeoid shrimp to a modern shrimp from the same superfamily (Feldmann and Schweitzer, 2010: Fig. 4); many muscle groups in the modern specimen could be identified on the fossil as well. Similarly, pleonal muscles in a Late Jurassic glypheid lobster and an Eocene stomatopod do not seem to differ much from modern representatives. Thus, morphologically similar specimens contain comparable muscles, which we refer to as “muscle conservatism”. Muscles in another marine arthropod, a horseshoe crab from the Late Jurassic of Germany, are also remarkably comparable to those in modern horseshoe crabs (Briggs et al., 2005).

Muscle attachment scars provide additional evidence for the presence, size, shape, and position of muscles. For ghost shrimps, the position and approximate size of closer muscle scars does not appear to have changed much through time (Hyžný and Klompmaker, 2015: Fig. 8). Unlike penaeoid and ghost shrimps, brachyurans have undergone a remarkable change in shape from longer than wide in the Jurassic, as in a lobster ancestor, to primarily wider than long in the Cenozoic combined with tucking of the pleon under the carapace (e.g., Glaessner, 1960; Guinot et al., 2013). This trend has led to a large reduction of muscles in the pleon and some reorganization of muscles in the carapace (e.g., Glaessner, 1960; Guinot et al., 2013). However, little is known about the evolution of muscle scars in the carapace of Brachyura throughout their evolutionary history. The same applies to several clades of Anomura that have evolved a crab-like morphology (Keller et al., 2015, 2017; Scholtz, 2014).

6. Conclusions and future directions

Our search into the literature has yielded 29 occurrences of muscles preserved in fossil malacostracans to which we add 18 new occurrences in the first overview of muscles in the malacostracan fossil record. Most of these occurrences are found in known Konservat-Lagerstätten. As our survey of malacostracan taxa with muscles preserved in Konservat-Lagerstätten has not been exhaustive, additional study of museum collections and new collecting efforts are expected to result in additional species with muscles preserved. More late Cenozoic species should be checked for the presence of muscles. It is possible that some specimens were overlooked because of a bias in research towards Mesozoic Konservat-Lagerstätten. Lithification and compaction should not have impacted late Cenozoic taxa as much as older specimens.

The muscles in the major cheliped propodi of a mid-Holocene ghost shrimp and the muscles in the pleon of a Late Devonian penaeoid shrimp are comparable to those of related modern specimens. Thus, for similarly-shaped body plans, we hypothesize conservatism in the evolution of musculature. Most changes in muscle structure may be
Fig. 14. Muscle scars in fossil decapod crustaceans as in Fig. 13, but with muscles marked. Inferred muscles: red = closer (adductor) muscles; light green = posterior gastric muscles; light blue = anterior gastric muscles; blue = attractor epimeralis muscles; yellow = antennar extensor muscles; pink = posterior gastric pits for stomach muscle; purple = internal mandible adductor muscles; orange = branchial muscles. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
expected for Brachyura, having undergone dramatic changes in carapace and pleonal shape since the Jurassic. Additional collecting of Brachyura from Konservat-Lagerstätten or re-examination of existing collections may yield specimens that can give clues about muscle development in true crabs. Future research could also focus on characterizing the preservation of muscles within and across species using many individuals to more quantitatively assess the relative preservation potential of muscles across the malacostracan body.

In the first overview of muscle scars in fossil malacostracans, our survey of 357 articles published from 2004 to 2006 and 2014 to 2016 yielded 162 occurrences with muscle scars on primarily internal molds. They are found most often on brachyuran carapaces and axiidean cheliped propodi. Nearly all occurrences are found from the Jurassic onwards in a variety of sedimentary settings and typically not in Lagerstätten. These scars are recognized by authors in only 19% (30) of the occurrences. Muscle scars are found in 24% (87) of the articles, suggesting that muscle scars are very common. This rich source of data can be used for many more studies on muscle scar presence, muscle identification, preservation, and evolution through time. Muscle scars can complement studies on muscle evolution through time, and may be particularly revealing for the shape changes associated with Brachyura.

Supplementary data to this articles (Appendices 1 to 3) can be found online at https://doi.org/10.1016/j.earscirev.2019.04.012.

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References


(Cenomanian) polychaete *Rollinschaeta myoplena* (Annelida: Amphinomidae).


